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THE EFFECTS OF FIRE BEHAVIOUR ON SECONDARY SUCCESSION IN BOREAL PINE STANDS: VEGETATION STRUCTURE, COARSE WOODY DEBRIS DYNAMICS AND SOIL CHARACTERISTICS.

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RÉSUMÉ DE LA THÈSE

En forêt boréale, le feu est considéré comme étant la plus importante perturbation naturelle. Il entraîne la mortalité des arbres, amorce des processus de succession, affecte la composition des espèces, détermine la séquestration du carbone et affecte la dynamique des nutriments. Le comportement du feu se traduit par sa magnitude, le moment où se produisent les processus après feu et la durée de ces processus. Les arbres exposés au feu peuvent subir des blessures au cambium/phloème, à la couronne et aux racines. Ces dommages dépendent en partie des différentes composantes du comportement du feu. La structure résultant de différentes intensités de feu peut déterminer les cycles des nutriments dans les forêts. En forêt boréale, une quantité considérable de matière organique est séquestrée dans les débris ligneux grossiers (DLG) et dans le bois enfoui.

Les objectifs généraux de cette étude étaient : 1) d'évaluer les mécanismes liés à la mortalité des arbres causée par le feu et d'analyser la distribution et la production des racines fines dans les peuplements de *Pinus sylvestris* reliés au comportement des feux; 2) d'évaluer les dynamiques simultanées des principales structures de peuplements durant la succession après un feu létal (FL) et de documenter la façon dont un feu non létal (FNL) affecte ces paramètres comparativement à un FL; 3) de documenter la disponibilité de nutriments et la séquestration de carbone des principales structures de peuplements liées à l'intensité d'un feu, le bois enfoui étant ici l'intérêt principal.

Dans les peuplements de pins sylvestres du nord de la Suède, la biomasse des racines de pins vivants et morts avec des degrés variés de blessures à la couronne ont été analysés une année après feu. La production de racines fines a été analysée par une expérience de croissance. Sur les sites brûlés, la mortalité des racines était plus élevée chez les arbres sévèrement brûlés, probablement liée à la profondeur de combustion de la matière organique du sol autour de ces arbres et non à une intensité plus forte du feu *per se*. La production de racines fines ne présentait pas de différences significatives entre les arbres qui n'étaient pas brûlés et ceux qui l'étaient. Cela suggère une priorité de la régénération racinaire après feu, probablement aux dépens de la croissance des tiges. La dynamique des racines après un feu a été rapportée par des facteurs directs et indirects. Les effets directs sont déterminés par la profondeur de la combustion de la matière organique du sol. Des effets indirects et permanents pourraient être causés principalement par les brûlures subies dans la zone de distribution des racines grossières près des troncs d'arbres, notamment par la perte du feuillage.

Les peuplements de pins gris (*Pinus banksiana* Lamb.) de l'Amérique du Nord sont généralement caractérisés par une structure équienne résultant de feux létaux (FL). Cependant, des feux non létaux (FNL) laissant des arbres sur pied vivants ont été rapportés.

Deux parties de l'étude ont été réalisées dans des peuplements de pins gris (*Pinus banksiana* Lamb.) du nord-ouest du Québec. Des peuplements de pins gris affectés par des FL et par des FNL ont été sélectionnés. Dans les peuplements, les caractéristiques des arbres, la structure d'âge, la biomasse du sous-bois, le volume et la biomasse des DLG ont été évalués; la biomasse du bois sec enfoui a été mesurée. L'azote total (N), le phosphore (P) et les nutriments échangeables ont été déterminés dans la litière forestière, le sol minéral et le bois enfoui.

La succession structurale des peuplements de pins gris à la suite d'un FL comprend trois étapes. L'ouverture de la canopée et la densité de pins gris ont diminué significativement avec le temps depuis un FL, alors que la densité d'épinette noire et le volume de DLG ont augmenté significativement. Comparativement aux FL, les FNL augmentent en moyenne la surface terrière des peuplements et réduisent la densité moyenne, retardent le remplacement du pin gris par l'épinette noire dans le couvert forestier, diminuent le volume de DLG et augmentent significativement la masse de bryophytes. Les FNL augmentent la diversité des arbres vivants tout en réduisant la diversité structurale des DLG.

Les concentrations de nutriments échangeables n'ont pas été significativement altérées après le feu dans les peuplements affectés par un FL. Dans les peuplements affectés par un FNL, l'azote, le phosphore et la capacité d'échange cationique ont présenté des différences significatives comparativement à ce que l'on trouve dans les peuplements affectés par un FL. Une courbe en forme de S décrit la séquestration de carbone le long d'un gradient de temps dans les peuplements affectés par un FL. Le sol minéral, la litière forestière et le bois enfoui sont les principaux réservoirs de carbone dans les peuplements affectés par un FL. Les FNL, dans les peuplements de pins gris, diminuent significativement la litière forestière et le réservoir de carbone constitué par le bois enfoui alors que la biomasse du sous-bois augmente du fait que celle des bryophytes double. Le bois enfoui a modifié les concentrations de nutriments dans le sol minéral adjacent, bien que cette action ait été à petite échelle.

L'étude confirme la diversité de l'amplitude de la perturbation naturelle, les processus de succession et le cycle de nutriments amorcé. Les résultats semblent pertinents pour un ajustement des systèmes d'aménagement forestier qui imitent les perturbations naturelles.

Mots clés : pin, feu, structure de peuplement, racines, bois mort.

INTRODUCTION GÉNÉRALE

0.1 Contexte

En forêt boréale, le feu est considéré comme étant le plus important agent naturel de perturbation à l'origine de la mortalité des arbres (Ryan et Reinhardt, 1988; Dickinson et Johnson, 2001). Amorçant le processus de succession des structures de peuplements et de la composition des espèces (MacLean et Wein, 1977; Engelmark et al., 1994; Schimmel et Granström, 1996; Johnson et al., 2000), cet agent influence la séquestration du carbone (Harmon, 2001; Rothstein et al., 2004) et la dynamique des nutriments (Brais et al., 2000; DeLuca et Sala, 2006) tout en créant les mosaïques forestières (Bergeron et al., 2004; Oliver, 1981).

Le régime de feux (intensité, sévérité, récurrence, intervalle entre les feux, étendue, etc.) détermine la diversité et l'amplitude du processus de repeuplement naturel (Johnson, 1992; Miyanishi, 2001; Sherriff et Veblen, 2006). L'intensité du feu est définie comme étant l'énergie physique d'un feu par unité de surface et de temps; la structure d'un peuplement résiduel à l'intérieur d'une zone incendiée est un indice de l'intensité d'un feu (Schimmel et Granström, 1996) Par ailleurs, cette intensité n'a pas d'influence directe sur la profondeur de la couche brûlée *sensu* Byram (1959). D'autre part, selon Johnson (1992), la sévérité de la combustion est reflétée par le niveau de changement environnemental causé par le feu lui-même, c'est-à-dire selon la mesure où le feu a affecté les structures de communauté écologique.

Les arbres exposés au feu peuvent présenter des blessures au cambium/phloème, à la couronne et aux racines (Ryan et Reinhardt, 1988; Ryan et Frandsen, 1991; Dickinson et Johnson, 2001; Bova et Dickinson, 2005). Le degré de combustion de la couronne varie selon l'intensité du feu et selon la hauteur et la taille de l'arbre (Van Wagner, 1973; Dickinson et

Johnson, 2001). La mortalité des racines est liée aux températures atteintes par le sol mais également à la profondeur d'enracinement (Swezy et Agee, 1991).

En écologie, la structure du peuplement est définie en termes de complexité et d'attributs structurels (McElhinny et al., 2005), dans lesquels les composantes structurelles clés sont : les arbres vivants, le bois mort, la végétation du sous-bois et la couverture morte. L'abondance et la taille de la variation des attributs de la composante structurelle fournissent des informations sur le développement du peuplement (Spies et Franklin, 1991; Acker et al., 1998; Wikstrom et Eriksson, 2000).

Basée sur les résultats de nombreuses études menées en forêt boréale, l'évolution de la structure de cette dernière à la suite d'un feu létal (FL), c'est-à-dire d'un feu de régénération (FR), peut être résumée en quatre étapes : 1) initiation des structures de peuplements; 2) exclusion des tiges avec autoéclaircie ; 3) rupture du couvert forestier, qui conduit parfois à l'amorce d'une nouvelle génération; et 4) établissement d'une vieille forêt, caractérisée par une forte diversité structurale (Oliver, 1981; Kenkel et al., 1997; Harper et al., 2005). Ces étapes sont caractérisées par une dynamique des débris ligneux grossiers (DLG) déterminés par un modèle « trajectoire en U » temporel (Harmon et al., 1986; Sturtevant et al., 1997; Brais et al., 2005; Harper et al., 2005). Au cours des premières années après feu, la composition du sous-bois faisant partie de la communauté pionnière est constituée de lichens, d'herbacés, de quelques espèces d'arbustes et un considérable tapis de bryophytes dans les vieux peuplements se développe (Foster, 1985; De Grandpré et al., 1993; Nguyen-Xuan et al., 2000; Fenton et Bergeron, 2006; Lecomte et al., 2006).

Les structures des peuplements (arbres vivants et morts, végétation du sous-bois, litière et DLG) exercent une forte influence sur le cycle de la matière organique de l'écosystème et sur celui des nutriments. Cette influence se traduit de différentes façons en fonction des particularités des espèces qui occupent le site. Ainsi, les recherches démontrent que l'épinette noire a un important impact sur les espèces d'arbres avec lesquelles elle entre en compétition, sur le sous-bois et sur les propriétés du sol (Arseneault, 2001; Lavoie et al., 2007). Les

espèces de sous-bois, telles que les bryophytes, peuvent emmagasiner une grande quantité de matière organique et de nutriments et modifier les propriétés du sol, augmenter son humidité et réduire sa température (MacLean et Wein, 1977; Oechel et Van Cleve 1986; Boudreault et al., 2002; Fenton et al., 2005). Les DLG et le bois enfoui sont caractérisés par une lente minéralisation des nutriments (Jurgensen et al., 1987; Crawford et al., 1997; Kayahara et al., 1996).

Les effets directs du feu sur le sol comprennent la perte de carbone et de nutriments sous l'action de la volatilisation et de la convection (MacLean et al., 1983, MacRae et al., 2001). Les effets indirects font référence aux modifications des propriétés physiques du sol (DeBano, 2000), à l'augmentation de la matière organique en décomposition (Rothstein et al., 2004), à la disponibilité des nutriments (Viro, 1974) et au lessivage (MacLean et al., 1983). Les effets immédiats du feu sur les concentrations de nutriments sont de courte durée dans les sols à texture grossière de la forêt boréale (Brais et al., 2000; DeLuca et al., 2002; Smith et al., 2004). Il en résulte que les structures de peuplements et leur abondance correspondant à différentes intensités de feu permettent de conclure à un cycle écosystémique de nutriments s'étendant sur une longue période.

Cette étude porte sur deux espèces de pin : pin gris (*Pinus banksiana* Lamb.) et pin sylvestre (*Pinus sylvestris* L.). Le pin gris est l'espèce de pin la plus répandue en Amérique du Nord (Ressources naturelles Canada, 2006). Il peut atteindre 20 m de haut. Habituellement, il pousse sur des sols sablonneux secs et acides. Le pin gris commence à montrer des signes de vieillissement à l'âge de 75 ans. Cette espèce décroît en fréquence à l'âge de 150 ans bien que certains individus dépassent 250 ans. Le pin sylvestre est l'espèce de pin la plus fréquente en Fennoscandinavie du Nord. Il pousse sur des sols sablonneux pauvres ou sur des affleurements rocheux. La longévité du pin sylvestre est de 250 à 300 ans. Toutefois, de plus vieux spécimens, dont certains ayant 700 ans, ont été rapportés. Ces deux espèces sont associées au feu. De plus, la reproduction du pin gris, du fait des cônes sérotineux qu'il produit, est favorisée par le feu (Gauthier et al., 1996). Le pin sylvestre, contrairement au pin gris, est considéré comme étant semi-résistant au feu.

0.2 Mécanisme de la mortalité des arbres causée par le feu

Dans les sols en forêt boréale, la pénétration de la chaleur est une fonction de la profondeur de combustion, qui est principalement contrôlée par la teneur en humidité et par la densité de combustible de la litière (Schimmel et Granström, 1996; Dickinson et Johnson, 2001, Miyanishi et Johnson, 2002). Les dommages occasionnés par le feu sur les racines peuvent affecter directement la vitalité des arbres par la réduction après feu de la consommation d'eau et d'éléments minéraux (Vogt et al., 1987; Persson, 1993; Dickinson et Johnson, 2001; Makkonen, 2001). La réserve de matière organique et d'éléments minéraux pour la croissance des racines pourrait être limitée s'il y avait un fort degré de détérioration du couvert forestier par le feu. Ainsi, la croissance des racines pourrait être directement liée au degré de défoliation causée par le feu. Peu d'études ont quantifié les dommages causés par le feu sur les racines et sur la dynamique ultérieure des racines. De plus, ces études, portant sur la dynamique des racines après feu, ont été effectuées 20 à 30 ans après le passage du feu tandis que notre étude a été entreprise seulement une année après feu. Aussi, il existe peu de connaissances relatives à la production de racines après un feu, particulièrement en relation avec les différents degrés de combustion du couvert forestier.

0.3 Impacts sur la structure de peuplement du pin gris

Le feu létal (FL) est le type le plus fréquent dans les peuplements de pins gris (*Pinus banksiana* Lamb.) du Canada. Le feu létal se caractérise par une forte intensité. Toutefois, la mortalité des arbres qui en résulte dépend aussi, des caractéristiques du peuplement avant le feu. Il est à l'origine des peuplements équiennes (Bergeron et Brisson, 1990; Johnson et al., 2000). Cependant, les recherches révèlent l'occurrence de forêts légèrement brûlées dans les peuplements de pins gris (Desponts et Payette, 1992 ; Gauthier et al., 1993; Weisberg, 2004). La présence de cicatrices caractéristiques sur les souches indique le passage d'un feu non létal (Sirois, 1993). Bien que quelques auteurs ont déjà décrit le développement d'un peuplement de pins gris après un FL (Gauthier et al., 1993; Sirois, 1993; Béland et al., 2003;

Hamel et al., 2004; Lecomte et Bergeron, 2005, Brais et al., 2005), il n'y a pas d'études reliées au développement simultané de structures importantes et au développement de diversité structurale après un FL. Aussi, dans plusieurs cas, la chronoséquence qui fait suite à un FL n'est pas longue et l'intervalle de temps entre le feu et les échantillonnages est trop étendu. À cause de ce long intervalle, il est possible que l'effet direct d'un FL sur le développement d'un peuplement de pins gris devienne impossible à identifier. De plus, il existe peu d'études portant sur l'influence des feux non létaux (FNL) sur les peuplements de pins gris dans le nord-ouest du Québec (ex. Arseneault (2001)).

0.4 Relations entre le type de feu, la structure des peuplements, l'accumulation de nutriments dans le sol et la séquestration du carbone

L'influence du feu sur les propriétés du sol et sur la séquestration du carbone dans les peuplements de pins gris a été étudiée par Rothstein et al. (2004), Hamel et al. (2004), Brais et al. (2000 ; 2005), Foster (1974), etc. Leurs résultats ont démontré que les effets immédiats du feu sur les concentrations de nutriments sont de très courte durée sur des sols boréaux à texture grossière (Brais et al., 2000 ; Rothstein et al., 2004), et l'amplitude des changements dans les nutriments du sol et dans les réservoirs de carbone dépend de la sévérité de la combustion de couverture morte (Brais et al., 2000). En fonction de l'âge des peuplements, des peuplements atteignent un état de vieille fôret caractérisée par une lente croissance d'organismes autotrophes et augmentent la rétention de carbone à cause de l'accumulation des détritus (Berg, 1986 ; Harmon, 2001; Chapin et al., 2002). Il a été suggéré que le feu joue un rôle rajeunissant en favorisant la minéralisation immédiate des nutriments, mais aussi en augmentant la séquestration du carbone à la suite du remplacement d'un peuplement âgé à croissance lente par un jeune peuplement à croissance rapide (Peet, 1992; Rothstein et al., 2004 ; Greene et al., 2007). La variation de l'intensité de feu dans une structure de peuplement peut entraîner une fluctuation dans la séquestration du carbone (Rothstein et al., 2004).

Il faut noter que le rôle du bois enfoui dans écosystèmes forestiers a été peu étudié. Les études ayant porté sur les peuplements mis en place selon un gradient de temps après feu permettent d'aborder les changements consécutifs pour ce qui est de la productivité des peuplements et du cycle des nutriments. Il existe plusieurs études ayant porté sur le régime du feu dans les peuplements de pins gris. Toutefois, la majorité des études ayant porté sur des peuplements de pins gris couvre une période de 40 à 90 ans après feu. Par conséquent, peu d'études ont porté sur le développement de jeunes et de vieux peuplements. L'influence des FNL sur les processus du sol et sur la séquestration du carbone dans les peuplements de pins gris n'a pas été étudiée. Bien que l'interaction entre les structures majeures de peuplements et les propriétés des sols a été discutée dans une étude de Brais et al. (2005), les peuplements qui se mettent en place après des FL et des FNL n'ont pas été séparés dans les modèles. Le rôle du bois enfoui dans le fonctionnement de l'écosystème du pin gris n'a pas été évalué. De plus, l'influence des FNL sur l'accumulation de bois enfoui et sur les propriétés et le cycle des nutriments est aussi inconnue.

0.5 Compte rendu des études et structure de la thèse

Mon projet d'études doctorales comprenait trois chapitres. Le **chapitre I** a porté sur les mécanismes de la mortalité des arbres causée par le feu. Dans les **chapitres II** et **III**, nous avons analysé l'impact du FL et du FNL sur la succession et la diversité structurales, sur la disponibilité des nutriments **et** sur la séquestration carbonée dans les peuplements de pins gris du nord-ouest du Québec. Dans cette étude, l'influence du type de feu sur la structure du peuplement et des processus connexes a été abordée sous différentes échelles. La mortalité des arbres consécutive au feu à l'échelle du peuplement est la résultante de l'effet additif de la mortalité individuelle des arbres. Toutefois, l'étude des effets de différentes intensités de feu à l'échelle de l'arbre (Chapitre I), lorsque les caractéristiques de l'arbre avant le feu sont mesurées, permet une meilleure compréhension de la mortalité des arbres causée par le feu à l'échelle du peuplement (Chapitre II). En même temps, la structure du peuplement résiduel et la succession qui fait suite à différents types de feux expliquent la séquestration carbonée et le cycle des nutriments dans l'écosystème (Chapitre III).

L'objectif global de cette thèse était de documenter les mécanismes de la mortalité des arbres causée par le feu, de documenter la structure de la succession du peuplement, la séquestration carbonée et l'accumulation des nutriments après un feu de régénération, c'est-à-dire un feu létal, (FL) dans des peuplements de pins de la forêt boréale, de comparer l'influence de la structure du peuplement sur l'accumulation de nutriments à la suite d'un feu létal et d'un feu non létal (FNL).

L'hypothèse générale de l'étude était que les différences liées à la magnitude du feu sont à l'origine des différences de la structure résiduelle du peuplement. Comparés aux FL, les FNL ont un effet rajeunissant sur les peuplements de pins gris en raison de leurs effets direct (minéralisation de la matière organique) et indirect (changements dans la structure des peuplements) sur la séquestration carbonée et le cycle des nutriments.

CHAPITRE I Distribution après feu des racines de *Pinus sylvestris* en rapport avec les caractéristiques du feu.

Smirnova, E., Bergeron, Y., Brais, S., Granström, A. 2008. « Post-fire root distribution of *Pinus sylvestris* in relation to fire behaviour », Canadian Journal of Forest Research, 38: 353-362.

Dans le premier chapitre, les **objectifs** étaient de quantifier la distribution spatiale des racines et la production de racines fines de pins sylvestres (*Pinus sylvestris L.*) suivant des degrés variables de dommages causés par le feu sur les couronnes. Nous avons posé comme hypothèse que l'impact destructif d'un feu sur les racines d'arbres serait double. Premièrement, la mortalité immédiate devrait être liée à la profondeur de combustion. Deuxièmement, la croissance des racines après un feu devrait être liée à la vigueur de l'arbre selon le degré de combustion de la couronne.

Le site d'étude décrit dans le **chapitre I** est situé dans des peuplements de pins sylvestres (*P. sylvestris L.*) du nord de la Suède. Quatre parcelles expérimentales ont été sélectionnées à l'intérieur de peuplements de pins sylvestres ayant échappé au feu en 2003 et quatre autres sur le territoire adjacent non brûlé (témoin).

Dans un peuplement brûlé, l'excavation des racines de deux arbres a été effectuée. L'influence du degré de combustion de la couronne sur la biomasse de racines a été basée sur l'approche expérimentale : dispositif avec contrôle des expériences. La biomasse de racines était estimée selon la méthode des monolithes. Dans ce chapitre, une méthode (échantillonnage de monolithes) a été utilisée pour analyser l'influence des feux sur la distribution des racines. L'efficacité de cette méthode a été démontrée dans plusieurs études (Böhm, 1979 ; Vogt et al., 1987 ; Persson, 1993; Messier et Puttonen,1993). Une approche expérimentale a été choisie pour évaluer la production de racines de pin après un feu. La méthode permet d'évaluer la production pendant une période bien déterminée. À cause des mailles qui constituent des obstacles physiques, le filet peut empêcher la pénétration des racines. Plus destructrice que le rhyzotron, cette approche est néanmoins beaucoup moins dispendieuse. Plusieurs recherches faisant appel à la méthode avec croissance ont donné des résultats fiables (Vogt et al., 1987; Makkonen et Helmisaari 1998).

Dans les **chapitres II** et **III,** les études entreprises ont été effectuées dans le nord-ouest du Québec, plus particulièrement dans la forêt boréale du sud-est du Canada. L'approche descriptive basée sur l'établissement d'une chronoséquence a été choisie. La chronoséquence de neuf peuplements de pins gris (*Pinus banksiana* Lamb.) (approximativement 10 ans d'intervalle) amorcée par des FL (feux létaux) a été établie sur une distribution équienne des âges dans le peuplement. De plus, dans le chapitre II, des données additionnelles représentant des peuplements issus de feux létaux de 149 et 155 ans ont été fournies par Nicolas Lecomte. À l'intérieur des peuplements affectés par un FL ou à proximité de ces derniers, huit peuplements qui ont survécu à un FNL (feu non létal) ont été choisis. Des cicatrices de feu caractéristiques situées au pied des arbres fournissent des signes évidents de FNL (Gutsell et Johnson 1996).

CHAPITRE II Influence de l'intensité du feu sur la structure et la composition des peuplements de pins gris dans la forêt boréale du Québec : arbres vivants, végétation du sous-bois et dynamique du bois mort.

Smirnova, E., Bergeron, Y., Brais, S. 2008. "Influence of fire intensity on structure and composition of jack pine stands in the boreal forest of Quebec: live trees, understory vegetation and dead wood dynamics". Forest Ecology and Management, 225: 2916-2927.

Dans le chapitre II, les objectifs de l'étude étaient : 1) d'évaluer les dynamiques communes et la structure de peuplement des arbres vivants, des DLG et de la végétation du sous-bois durant la succession qui fait suite à un FL; et 2) de documenter la façon dont un FNL altère la dynamique et la diversité de ses constituants structuraux. Pour mener cette étude, nous avons posé les deux hypothèses suivantes : 1) un FNL entraîne un rajeunissement de la structure du peuplement par ralentissement de la sénescence du peuplement; et 2) un FNL augmente de façon plus importante la diversité structurale du peuplement qu'un FL.

CHAPITRE III Influence du feu létal et non létal sur l'accumulation des nutriments dans le sol et la séquestration carbonée le long d'un gradient après feu de peuplements de pins gris de la forêt boréale. "Influence of stand-replacing and non-stand replacing fire on soil nutrient accumulation and carbon sequestration along a post-fire successional gradient in boreal jack pine stands."

Les résultats de l'étude présentée dans ce chapitre ont été soumis à la « Revue canadienne de recherche forestier ».

Les objectifs du troisième chapitre étaient : 1) de documenter la séquestration carbonée dans la biomasse vivante et morte et dans le sol minéral; de documenter la disponibilité des nutriments du sol le long d'une chronoséquence de peuplements de pins gris après un FL; 2) de comparer la séquestration carbonée et le statut des nutriments du sol entre des peuplements affectés par des FL et ceux ayant connu des FNL; 3) d'estimer la différence entre le sol

forestier et les propriétés chimiques du bois enfoui et de documenter l'influence du bois enfoui sur les propriétés minérales du sol; 4) d'estimer l'influence de la structure du peuplement, spécialement le bois enfoui, sur la matière organique et l'accumulation de nutriments après deux types de feux. Les hypothèses du chapitre III étaient les suivantes : 1) les FNL qui induisent des changements dans les structures de peuplements réduisent le stock de C issu des débris comparativement aux FL; 2) les concentrations de nutriments échangeables ne sont pas altérées par des FNL; 3) au niveau du sol minéral, le bois brûlé peut entraîner un accroissement de la concentration en nutriments sur une petite échelle.

Pour recueillir les données des chapitres II et III, l'approche descriptive basée sur la chronoséquence après un feu a été utilisée. L'avantage de cette approche est qu'elle permet de recueillir des données couvrant de longues périodes en un temps réduit. Cependant, pour obtenir des résultats fiables, la sélection des peuplements doit être effectuée de façon très vigilante, car ces peuplements doivent répondre à des propriétés environnementales similaires. En outre, plus le nombre de répétitions est élevé, plus les résultats sont fiables. Un problème se pose avec les FNL parce qu'il est presque impossible d'avoir des peuplements d'âge semblable qui ont subi ce FNL au même moment.

Dans les chapitres II et III, les méthodes conventionnelles d'évaluation des caractéristiques des arbres vivants et morts ont été appliquées. L'ouverture de la canopée a été estimée par les photographies hémisphériques. La biomasse de la végétation du sous-bois a été échantillonnée au niveau du sol. Pour atteindre les objectifs du chapitre III, le poids des DLG et du bois enfoui sec a été mesuré. L'azote total, le phosphore et les nutriments échangeables ont été déterminés dans la litière forestière, le sol minéral et le bois enfoui.

Le pin gris est l'une des espèces dominantes de la forêt boréale du Canada. Cette espèce présente un grand intérêt pour l'industrie forestière. L'approche d'aménagement écosystémique a pour but d'imiter la variabilité inhérente aux dynamiques de la perturbation naturelle (DeLong and Tanner, 1996; Harvey et al., 2002; Bergeron et al., 2007). Toutefois,

la compréhension de la variabilité de la magnitude de la perturbation naturelle est un élément clé pour l'ajustement des pratiques sylvicoles.

CHAPITRE I

POST-FIRE ROOT DISTRIBUTION OF PINUS SYLVESTRIS IN RELATION TO FIRE BEHAVIOUR

Dans ce chapitre, les mécanismes entraînant la mortalité des arbres à la suite d'un feu de forêt seront abordés. Spécifiquement, le chapitre portera sur la mortalité et la croissance racinaire post incendie. À travers cette étude, nous souhaitions valider l'hypothèse stipulant que la vitalité des arbres restants serait dépendante de la variation d'amplitude dans le comportement du feu. L'étude a été menée dans des peuplements de pins sylvestres (*Pinus sylvestris* L.) du nord de la Suède. Les impacts du feu ont été évalués par l'excavation du réseau racinaire grossier, par la mesure de la biomasse en racines fines et par une expérimentation sur le terrain qui visait l'évaluation de la croissance racinaire après feu.

1.0 Abstract/Résumé

Fire can potentially have a large direct impact on tree roots and thus contribute to reduced tree vitality. Tree canopy status after fire should have an impact on the post-fire production of fine roots, further affecting root function. We analyzed the standing crop of live and dead roots in *Pinus sylvestris* with varying degrees of crown scorch, one year after fire in northern Sweden.

On the burnt sites, total *Pinus* live fine root biomass was 74% of that at the control sites, and for roots <2 mm it was only 19% of the control, indicating an 80% reduction due to fire. Root mortality was highest for high-scorch trees, but this was probably due to higher depth of burn in the organic soil for these trees, and not to higher fire intensity *per se*. Fine-root production was also assessed by an in-growth experiment. This showed relatively similar fine-root production in both control trees and fire-damaged trees, indicating a high allocation to root growth for the damaged trees, to make up for lost root function.

[1]Smirnova, E., Bergeron, Y., Brais, S., Granström, A. 2008. «Post-fire root distribution of *Pinus sylvestris* in relation to fire behaviour », Canadian Journal of Forest Research, 38: 353-362.

Root dynamics after fire are related to a number of factors, and direct effects are determined by the depth of burn in the organic soil layer. Indirect, long-lasting effects could be due mainly to girdling of coarse roots close to tree stems and canopy loss.

Keywords: fire, boreal forest, root biomass, fine roots

Le feu peut potentiellement avoir un important impact sur les racines des arbres et contribue ainsi à réduire leur vitalité. L'état du sous-bois après un feu devrait avoir un impact sur la production de racines fines après feu, après avoir affecté la fonction des racines. Nous avons analysé la biomasse des racines vivantes et mortes dans des peuplements de pins gris avec des degrés variés de blessures à la couronne une année après un feu dans le nord de la Suède.

Dans les sites brûlés, la biomasse totale de racines fines de *Pinus* vivants représentait 74 % de ce que l'on a trouvé dans les sites de contrôle; les racines constituant moins de 2 mm, c'était seulement 19 % des sites de contrôles, ce qui représente une diminution de 80 % causée par le feu. La mortalité des racines était plus forte chez les arbres brûlés sévèrement, mais cette situation était probablement causée par la plus grande profondeur de combustion dans le sol organique de ces arbres et non à l'intensité plus élevée des feux *per se*. La production de racines fines était aussi analysée par une expérience de croissance. Cela a montré une production de racines fines relativement similaire dans les arbres situés dans les sites de contrôle et dans les arbres endommagés par le feu, ce qui indique une forte allocation de croissance de racine chez les arbres endommagés. Les dynamiques des racines après un feu sont liées à plusieurs facteurs, et les effets directs sont déterminés par la profondeur de la combustion dans la couche de sol organique. Les effets indirects à long terme pourraient être principalement causés par la combustion de la ceinture de racines grossières près des troncs d'arbre et par la détérioration de la couronne.

Mots-clés : feux, forets boréale, biomasse racinaire, racines fines

1.1 Introduction

Trees exposed to fire can suffer injury to the cambium/phloem, to the crown and to the roots, and these three damage types depend partly on different components of fire behaviour (Ryan and Reinhardt, 1988; Dickinson and Johnson, 2001; Hély *et al.*, 2003). As for cambial damage, it depends on the bark thickness and duration of the heating (Bova and Dickinson, 2005; Ryan and Frandsen, 1991; Martin, 1963). In contrast, the degree of crown scorch is

more directly related to fire intensity and the height of the tree, because of the short exposure time needed to kill small-sized leaves (Van Wagner, 1973; Dickinson and Johnson, 2001). Finally, root mortality would relate to the amount of soil heating and the depth distribution of roots (Swezy and Agee, 1991). For boreal soils with a well-developed organic humus layer, heat penetration is a function of the depth of burn, which is controlled mainly by the moisture content of the forest floor (Schimmel and Granström, 1996; Dickinson and Johnson, 2001; Miyanishi and Johnson, 2002).

It is obvious that root damage from fire can impact upon tree vitality directly by reducing post-fire uptake of water and mineral nutrients (Dickinson and Johnson, 2001), but there are still few studies quantifying fire-damage to roots and the subsequent root dynamics. Swezy and Agee (1991) found that fine-root mass had decreased by 75% within 5 months after burning of old-growth *Pinus ponderosa*. Loss was most pronounced in organic soil and in the upper 10 cm of mineral soil. They reported a high degree of smoldering in the organic soil layer, due to high litter accumulation close to the stems, although most of the root loss appeared to have occurred between 1 and 5 months after the fire, i.e. was not due to direct heat kill (Swezy and Agee, 1991).

Fine-roots are inherently dynamic, with substantial annual production (Vogt *et al.*, 1987; Persson, 1993; Makkonen and Helmisaari, 1998). After fire, this would be expected to be even higher, due to the need to recuperate lost root function. On the other hand, carbon supply for root growth could be limiting, particularly if there has been a high degree of canopy loss in the fire. Consequently, root growth could be directly related to the degree of fire-caused defoliation. Not much is known of post-fire production of roots, however Sayer and Haywood (2006) found little impact of fire on fine root production in *P. palustris*, but their stands had been repeatedly burnt at three year intervals, and there was little foliage damage from the fire.

The impact of sub-lethal fire on tree roots would be expected to be two-fold. First, immediate mortality should be related to depth of burn. Second, post-fire growth of roots

should be related to vitality of the tree, largely following the degree of crown scorch. In order to analyze these relationships, we quantified the spatial root distribution and fine-root production for Scots pine (*P. sylvestris* L.) with varying degrees of crown damage from fire.

1.2 Study area and sampled trees

Our study area is located in the north of Sweden within the Northern Boreal zone. On 17 July 2003 two fires, 8 km apart, were ignited by lightning (approx position 64°00'N, 20°45'E). There was a long drought period prior to the fires (virtually no precipitation for 30 days prior to July 17). Each fire eventually covered 115-120 ha before being suppressed. The tree layer within the burns is dominated by *Pinus sylvestris* L. and the understory vegetation of the area is of mesic *Vaccinium* and dry lichen-shrub types. The climate has a continental character with an average yearly precipitation of 800 mm, and a growing season that lasts 120-150 days starting in the beginning of June (Sveriges klimat, 2007). The bedrock consists of different granites and is covered by a sandy moraine. The soil is of iron-podzol type and is of relatively low fertility.

Within these burns and on adjacent unburned terrain we located four pine stands of similar age (c. 40 yr.) and density on flat, relatively stone-free ground. Of four selected stands two were burnt and two unburned (control) stands; unburned stands were located in the vicinity of the burned ones. The stands had regenerated naturally from seed trees after clear-felling. They had been subject to pre-commercial thinning, but no management in the last ten years.

1.2.1 Coarse root structure and damage pattern

In order to have a general picture of the mechanisms of fire impact on coarse (diameter >10 mm) pine roots in relation to root architecture, the root system of two scorched pine trees were excavated in one of the stands in August 2004, i.e. one year after the fire.

The soil was carefully removed from all coarse roots within a circle, starting from the tree. During excavation we mapped, took photos and documented the status of each root along its length: its depth and position in the soil horizon, status of bark and cambium (color, fungal and insect attack), and presence of stones adjacent to the root. This part of the study was completed in order to better understand the mechanisms of root mortality, although no quantitative analysis was done.

1.2.2 Fine-root biomass measurements

In July 2004 we selected, within each of the burned areas (B1, B2), 4 pine trees that had been subject to a low degree of crown scorch (more than 50% of the canopy remaining) and 4 trees that had been subject to a high degree of crown scorch (30-40% of the canopy remaining), for a total of 16 burned trees. On each of the unburned adjacent sites (C1, C2) we selected 3 control trees. In order to minimize the quantity of roots from "non-target" trees, we choose trees with a minimal distance of 3 m between the studied tree and any neighbouring trees.

The following characteristics were documented for the selected trees: height, DBH, scorch height (heat-killed foliage), height of char on two sides of the tree (uppermost and lowermost char height) and bark thickness at 1.3 m height (Table 1.1). The composition of the understory vegetation was documented by visual estimation of the selected trees. At each tree, soil monoliths for quantification of fine-root biomass were taken along two transects; one on the side of the highest charring of the tree stem and one on the opposite side. Along each transect three monoliths were taken in the following positions: 1) close to the tree stem (10 to 20 cm from the stem), 2) half way between the tree stem and the edge of the canopy projection (50 to 70 cm from the stem, depending on size of the tree) and 3) at the edge of canopy projection (80 – 130 cm from the stem). The soil monoliths had a surface area of 25 x 25 cm and were taken down to 20 cm in the mineral soil. Each monolith was separated

into three horizons: organic soil layer, upper mineral soil layer (0 - 10 cm) and lower mineral soil layer (10 - 20 cm). Depth of the charcoal/ash layer and of the residual humus layer was measured on four points along the sides of each monolith. Thus, we sampled in total 22 trees and around each tree we took 6 forest floor samples and 12 mineral soil samples (two mineral soil horizons).

Table 1.1 Site information: tree characteristics

Scorch class	DBH (cm) / sd	Tree Height (m) / std	Scorch height			Mean tree bark thickness (cm) / sd
			mean stem upper char height (cm) / sd	mean scorched crown (m) / sd	mean non scorched crown (m) / sd	
Control (n=6)	16.06/ 0.8	11.1/ 2.3	absent	absent	6.65 / 0.7	1.07 / 0.6
Low-scorch (n=8)	17.32/ 0.9	10.5/ 2.7	84.62/ 173.9	2.16 / 8.8	4.81 / 4.4	0.91 / 0.5
High-scorch (n=8)	16.14/ 0.9	9.7/ 1.8	74.5/ 149.6	3.32 / 1.1	2.61 / 1.3	1.16 / 0.7

n: number of trees; sd: standard deviation

1.2.3 In-growth experiment

Pine fine-root production was assessed by the in-growth bag method (Messier and Puttonen, 1993; Makkonen, 2001). In one of the burned sites and in the adjacent control site, 3 trees of each scorch severity class, described in "fine-root biomass measurements" above, were selected. Cylindrical nylon mesh bags (7 cm diameter, 20 cm long) were filled with 2 mm sieved sand. The mesh size of the bags was 2 mm. Holes of approx. 8 cm diameter were made with a cylindrical corer along the transects at the three different distances described above. At the end of the vegetation season (August 2004), one mesh bag was placed into each hole and covered to a depth of 1 cm with organic material taken from the adjacent soil surface. Thus in total we installed 54 mesh bags. Fourteen months later, in October 2005, we were able to recover only 32 of these. The rest were lost due to animal destruction of the markers indicating the bag location.

1.2.4 Laboratory methods

The monoliths were brought into the laboratory where they were kept at 4 °C. They were then cut into several pieces to facilitate the extraction of roots. The soil was carefully removed from the roots of each monolith piece; afterwards all roots were washed free of soil with cold water. Pine roots were further separated from the others. Root characteristics such as colour, smell, taste, and presence of resin were used for pine root identification (Vogt *et al.*, 1987; Messier and Puttonen, 1993; Finér *et al.*, 1997; Makkonen 2001). Presence and status of ectomycorrhiza (live, dead) was noted. Then pine roots were sorted into live and dead roots according to the following diameter classes: <1 mm, 1 – 2 mm, 2 – 5 mm, 5 - 10 mm, > 10 mm (Vogt *et al.*, 1987; Makkonen, 2001). The extracted roots were then dried (24 h, 36 ° C) and weighed. Texture of the mineral soil from the monoliths was assessed by sieving.

The in-growth samples were sorted in the laboratory into species without separation into size classes and with no separation between dead and live roots.

1.2.5 Statistical analysis

Data analyses were done using the SAS statistical package (SAS Institute Inc. 1988). We used a three-way analysis of variance (ANOVA) with the general linear model (proc GLM) procedure (Lindman 1974; Legendre and Legendre 1998) to test for effects of site, scorch class and distance from stem on forest floor thickness and the influence of scorch class and distance from stem on charred layer thickness. A preliminary ANOVA with fixed factors (scorch class and scorch side) showed that there was no significant difference in forest floor and charred layer thickness between the low-char side and the high-char side of the trees ($p > 0.05$). Therefore, forest floor thickness values from both tree sides were pooled. Square transformation was applied to the forest floor thickness values in order to satisfy the residual normality assumption (proc univariate), whereas charred layer thickness satisfied the assumption without transformation. The interaction effects among forest floor or charred layer thickness and site, scorch class and distance were tested; the site variable has been treated as a random factor.

A three-way analysis of variance (ANOVA) was performed using the SAS GLM procedure to test for possible effects of site, scorch class and distance from stem on root biomass. Different transformations were tested to satisfy the assumptions of normality and homogeneity of variances. Finally summed and ranked biomass (proc rank): of <1 and 2 mm live (L<2 mm) and dead roots (D<2 mm); biomass of live (L2-10 mm) and dead roots (D2-10 mm) of 2 mm, 2 - 5 mm, 5 - 10 mm and >10 mm diameter classes; and ranked total live (sumLR) and dead root biomass (sumDR) respected the residual normality assumption. A preliminary ANOVA with fixed factors (scorch class and scorch side) confirmed that there was no significant difference in root biomass between the low-char side and the high-char

side of the trees ($p > 0.05$). Therefore, ranked root biomass values from both sides of the stems were pooled.

A two-way analysis of variance (ANOVA) was performed using the SAS GLM procedure to test for possible effects of scorch class and distance from stem on pine root production in the in-growth experiment. Note that the in-growth experiment was conducted in only one of the burned sites and the control site adjacent to it, therefore the site variable has not been included into the model. As almost half of the in-growth samples were missing, the in-growth biomass from each tree was pooled according to the corresponding distances. Pine root production values satisfied the normality assumption without transformation.

Root biomass and root production analyses were applied for each soil horizon separately. Interaction effects among root biomass and root production and environmental variables were tested. The site variable was randomized for all ANOVAs. All factor effects and their interactions were tested using Type III SS outputs.

Forest floor and charred layer thickness, and live and dead root biomass were subjected to Tukey's multiple comparison tests to determine if differences among distances from the stem were significant. As most of the interactions between root biomass, forest floor and charred layer thickness of different scorch classes and corresponding distances were significant Tukey's test was also conducted for each scorch class.

1.3 Results

1.3.1 Fire impact on the forest floor

The understory vegetation cover of the control sites was dominated by Ericaceous species: *Calluna vulgaris* (40%), *Empetrum hermaphroditum* (32%) and *Vaccinium* spp. (24%). In the burned sites, understory vegetation was almost completely lacking at the time of sampling. There was only sparse recruitment of *Deschampsia flexuosa,* and *Luzula pilosa* and an occasional *Vaccinium* spp. Mean forest floor thickness below the canopies in the control sites was 6.7 cm (Table 1.2) and forest floor thickness was significantly higher near the stems than at the middle and edge of the canopy projection (Table 1.3; Fig. 1.1). In the burned sites, mean forest floor thickness differed between scorch classes.

Table 1.2 Site information: soil characteristics

Scorch class	Mean forest floor thickness (cm) / sd	Mean charcoal layer thickness (cm) / sd	Gravel >16 mm (%) content / sd	Coarse sand 5.6-1.6 mm (%) content / sd	Fine sand 0.56-0.16 mm (%) content / sd
Control (n=6)	6.67 / 2.7	absent	5.35 / 2.1	30.03 / 14.6	64.39 / 14.2
Low-scorch (n=8)	4.33 / 0.71	4.34/ 0.71	4.59 / 4.1	19.34 / 19.2	75.64 / 20.7
High-scorch (n=8)	1.36 / 0.17	3.74 / 0.32	5.95 / 3.3	27.08 / 13.9	66.97 / 14.6

n: number of trees; sd: standard deviation

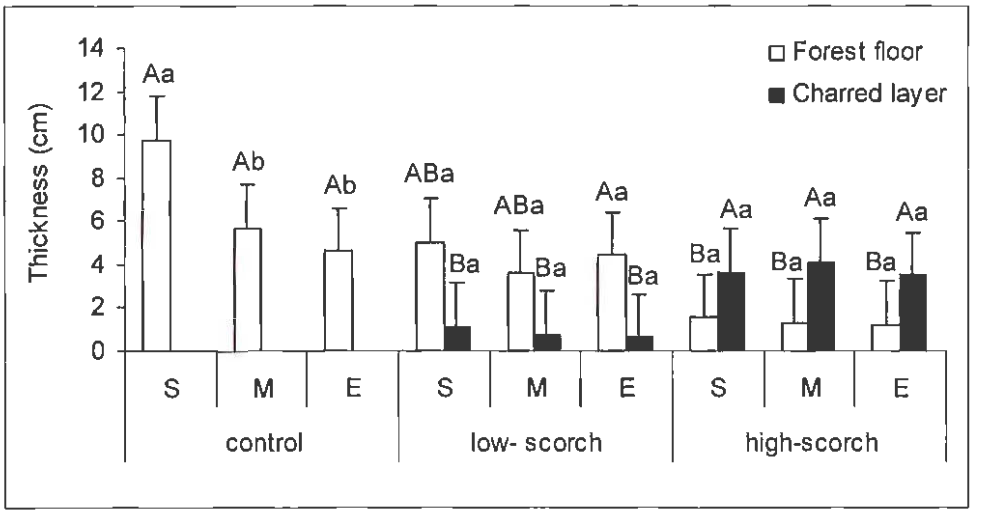

Fig. 1.1 Mean floor and charcoal thickness (cm) along the gradient from the stem: S-near stem; M-middle; E-edge. Tukey's multiple comparison tests of forest floor square–transformed mean and charred layer mean thickness among scorch classes and distances. Note: capital letters indicate differences among the corresponding distances of different scorch classes, and lower case letters indicate differences among distances within the same scorch class. Thicknesses with the same letters are not significantly different. Error bars are SDs

This difference was most pronounced near the stem. For low-scorch and high-scorch trees the mean thickness of the forest floor did not differ with distance from the stem. There was a statistically significant difference in mean thickness of the charred organic soil between low-scorch and high-scorch trees (Table 1.3; Fig. 1.1). There was no statistically significant difference in thickness of the charred layer with distance from stem, for either the low-scorch or for the high-scorch class.

Table 1.3 Results from the ANOVA completed on square-transformed forest floor thickness of control, low-scorch and high-scorch trees; and charred layer thickness performed on low-scorch and high-scorch trees.

Source	Forest floor thickness			Charred layer thickness		
	DF	*F*	*p*	DF	*F*	*p*
Overall model	17	3.08	<0.01	14	4.94	<0.01
Error	113			84		
Site	1	2.38	0.13	1	0.15	0.70
Scorch class	2	5.18	<0.01	1	45.42	<0.01
Distance	2	0.73	0.48	2	1.61	0.21
Site*Scorch class	2	5.16	<0.01	2	1.05	0.35
Site*Distance	2	0.09	0.91	2	3.04	0.05
Scorch class* Distance	4	4.57	<0.01	3	0.41	0.66
Site*Scorch class* Distance	4	1.98	0.10	3	0.08	0.93

1.3.2 Coarse–root architecture

The two trees we sampled for coarse-root architecture had a diameter at breast height of 10.5 and 14.5 cm respectively. Most coarse roots were found within approx. a 50 cm radius from the stem, and roots had a diameter of 2-8 cm at their point of attachment to the root collar. There was a maximum of 6 major tap roots (diameter of each at the collar of approx. 10 cm), and one vertically oriented anchor root of approx. 50 cm depth. Bark thickness of coarse roots did not exceed 2 mm.

Most of the laterally oriented coarse roots were located in the mineral soil or at the interface of the humus and mineral soil. These roots with the upper part of the cambium/phloem located in the humus layer had in many cases been heat-damaged during the fire, whereas the lower side was unaffected and still intact. These initially heat-damaged zones were easily identified, because of the charred bark and dark cambium colour.

There were also instances where a short section of the root showed evidence of complete heat-girdling, whereas the posterior parts had escaped heat damage. These parts were thus cut-off from phloem transport and were dying. At the time of sampling (one year after fire), the inner bark of these cut-off roots had started to die and was easily peeled off, but was still distinct from those sections that had been directly heat-killed.

There were several instances where roots growing over large stones in the mineral soil surface had been heat-killed, because of the lack of the protection of the mineral soil from the heat.

1.3.3 Quantity and spatial distribution of roots

Live-roots

For control trees live fine-root mass of L2-10 mm diameter class was significantly higher near the stem than at the middle and edge of the canopy projection (Figs. 1.2a, b; Table 1.4), but this was mainly due to a decrease in the larger size fractions with distance from the stem. Further, there was a marked decrease in root mass with depth, particularly for finer root fractions: control trees had the largest quantity of roots with diameter less than 1 mm in the organic soil layer, lower in the upper mineral soil and very low in the lower ($10-20$ cm) mineral soil. Abundant ectomycorrhiza was observed on the control tree fine-roots in the humus layer.

For trees at the burnt sites, mass of fine roots L<2 mm was very low in all soil horizons compared to control trees (Fig. 1.2a). For larger size fractions the difference was not as dramatic. Thus, both high-scorch and low-scorch trees had significantly lower fine-root mass than control trees for all soil horizons, and in many cases fire significantly decreased root mass also of diameters more than 2 mm. Total live root mass of the high-scorch trees was only a third of that of the control trees, whereas low-scorch and control trees did not differ

(Fig. 1.2a, b, Table 1.4). Similar to control trees, scorched tree root mass was higher near the stems than further out. Distance from low-scorched trees significantly influenced fine-root (L<2 mm) mass (Table 1.4; Fig. 1.2a, b)

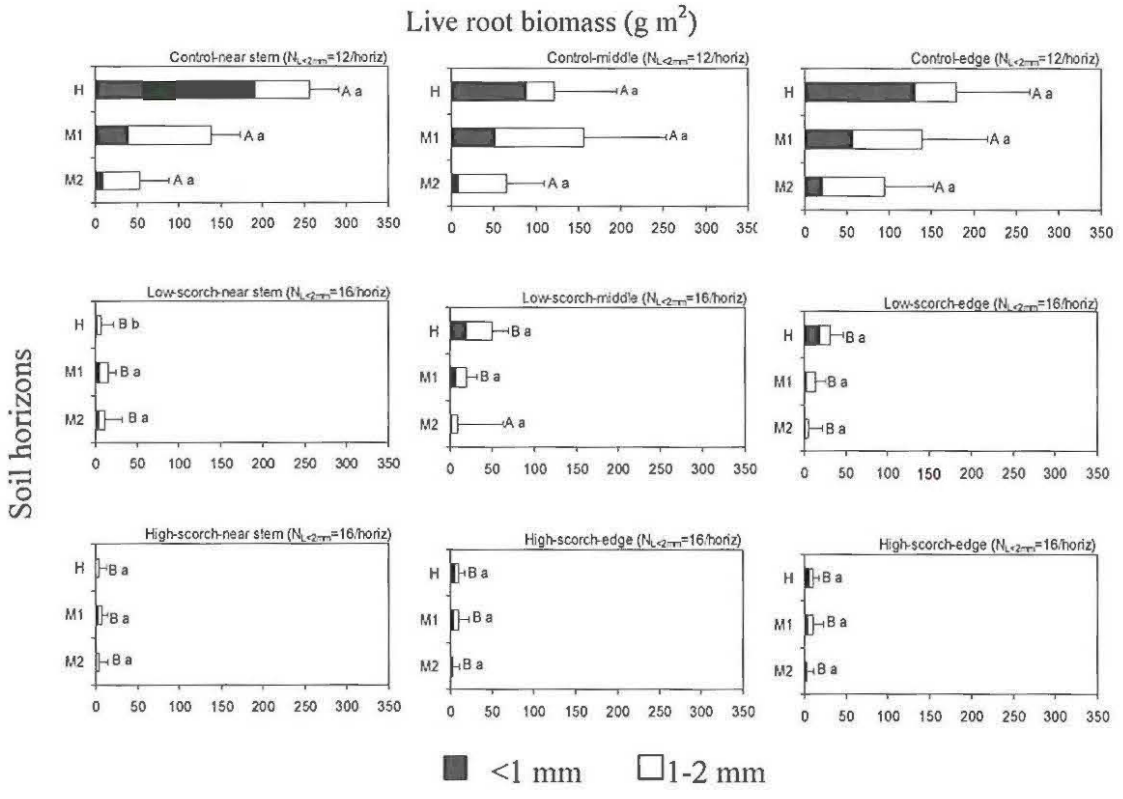

Fig. 1.2a Mean live root biomass (g·m^{-2}) to diameter L<2 mm. Tukey's multiple comparison tests of L<2 mm (<1 mm+2 mm) biomass rank mean among scorch classes and distances. Note: capital letters indicate differences among the corresponding distances of different scorch classes, and lower case letters indicate differences among distances within the same scorch class. Biomasses with the same letters are not significantly different. Error bars are SDs

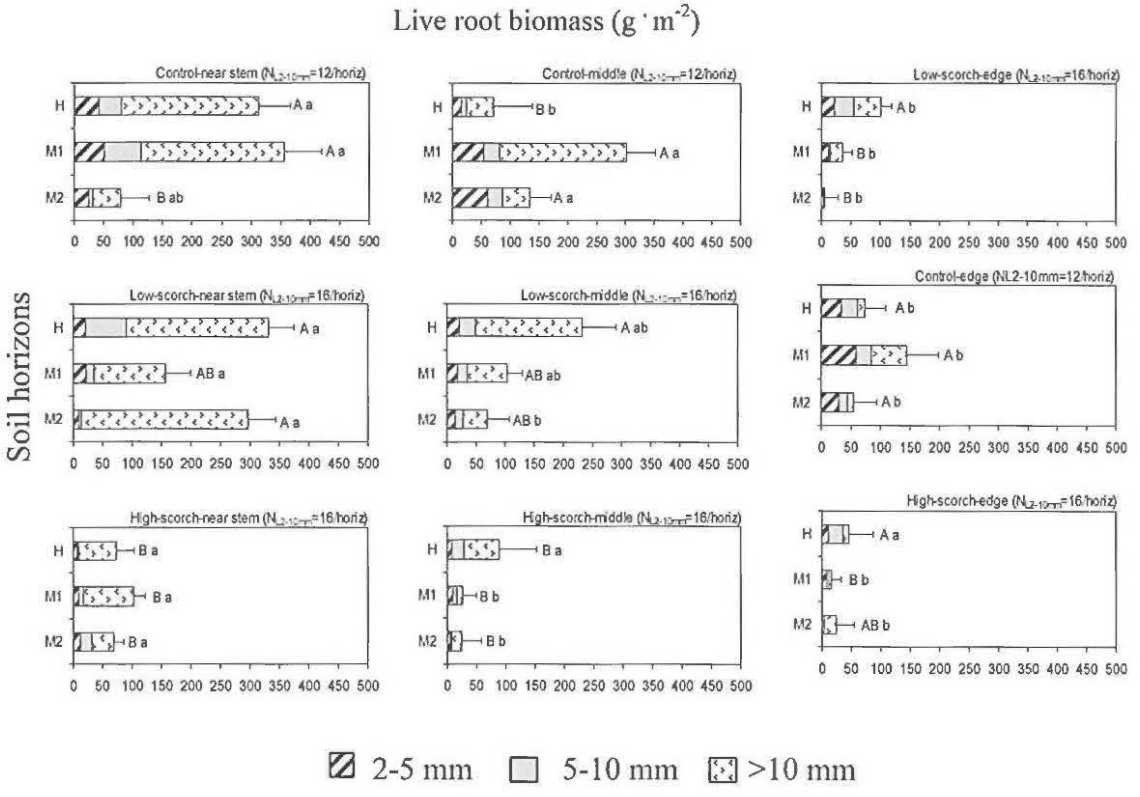

Fig. 1.2b Mean live root biomass ($g \cdot m^{-2}$) to diameter L2-10 mm. Tukey's multiple comparison tests of L2-10mm (2-5 mm+5-10 mm+>10 mm) biomass rank mean among scorch classes and distances. Note: capital letters indicate differences among the corresponding distances of different scorch classes, and lower case letters indicate differences among distances within the same scorch class. Biomasses with the same letters are not significantly different. Error bars are SDs

Table 1.4 Results from the ANOVA performed on ranked diameter classes of live-root biomass

Soil horizon	Source		L<2 mm		L2-10 mm		Sum LR	
		DF	*F*	*p*	*F*	*p*	*F*	*p*
Organic horizon	Overall model	17	7.56	<0.01	1.51	0.03	3.5	<0.01
	Error	114						
	Site	1	1.91	0.17	2.55	0.11	1.91	0.17
	Scorch class	2	52.69	<0.01	6.13	<0.01	21.84	<0.01
	Distance	2	0.25	0.78	2.62	0.04	3.12	0.04
	Site*Scorch class	2	2.73	0.06	2.24	0.08	3.02	0.05
	Site*Distance	2	0.25	0.78	0.38	0.69	0.30	0.74
	Scorch class* Distance	4	9.87	0.03	1.55	0.07	1.82	0.07
	Site*Scorch class* Distance	4	0.47	0.75	0.72	0.58	0.12	0.98
Upper mineral horizon	Overall model	17	6.84	<0.01	3.15	<0.01	5.18	<0.01
	Error	114						
	Site	1	0.16	0.69	1.23	0.27	0.21	0.65
	Scorch class	2	18.12	<0.01	12.79	<0.01	21.95	0.01
	Distance	2	0.11	0.89	7.94	0.02	2.82	0.05
	Site*Scorch class	2	31.99	<0.01	7.74	0.01	11.18	<0.01
	Site*Distance	2	0.02	0.98	1.20	0.31	0.94	0.39
	Scorch class* Distance	4	12.14	0.03	8.43	0.01	10.07	0.01
	Site*Scorch class* Distance	4	0.23	0.92	0.44	0.78	1.09	0.37
Lower mineral horizon	Overall model	17	4.55	<0.01	4.74	<0.01	4.21	<0.01
	Error	114						
	Site	1	8.56	<0.01	20.13	<0.01	18.54	<0.01
	Scorch class	2	15.88	<0.01	7.38	<0.01	10.17	<0.01
	Distance	2	0.16	0.85	2.13	0.05	1.66	0.09
	Site*Scorch class	2	14.13	<0.01	13.13	<0.01	8.60	<0.01
	Site*Distance	2	0.89	0.41	0.85	0.43	1.34	0.27
	Scorch class* Distance	4	5.06	0.03	6.31	0.04	3.64	0.06
	Site*Scorch class* Distance	4	0.36	0.84	2.10	0.08	1.59	0.18

There was no significant difference either in root mass or in the depth of burn between the two different sides of the sampled tree (windward and leeward sides). Little ectomycorrhiza was found on the fine roots of low-scorch trees in the forest floor, and only some remnants of dead ectomycorrhiza were left on the roots of severely scorched trees.

Dead roots

For the control trees the quantity of dead roots was less than 5% of that of live roots. For low-scorch and high-scorch trees the quantity of total dead roots (sumDR) was 41% and 82% of that of total live roots, respectively; and for roots D<2 mm the proportion of dead roots was even higher 160% and 317% respectively (Figs. 1.3a, b). Dead root mass of highly-scorched trees was approx. 20 times higher than that of the control. Dead-root biomass of all classes and of the total dead root biomass differed significantly among scorch severity classes (Table 1.5). A substantial amount of dead roots were also found at a depth of 10-20 cm (horizon M2) in the mineral soil.

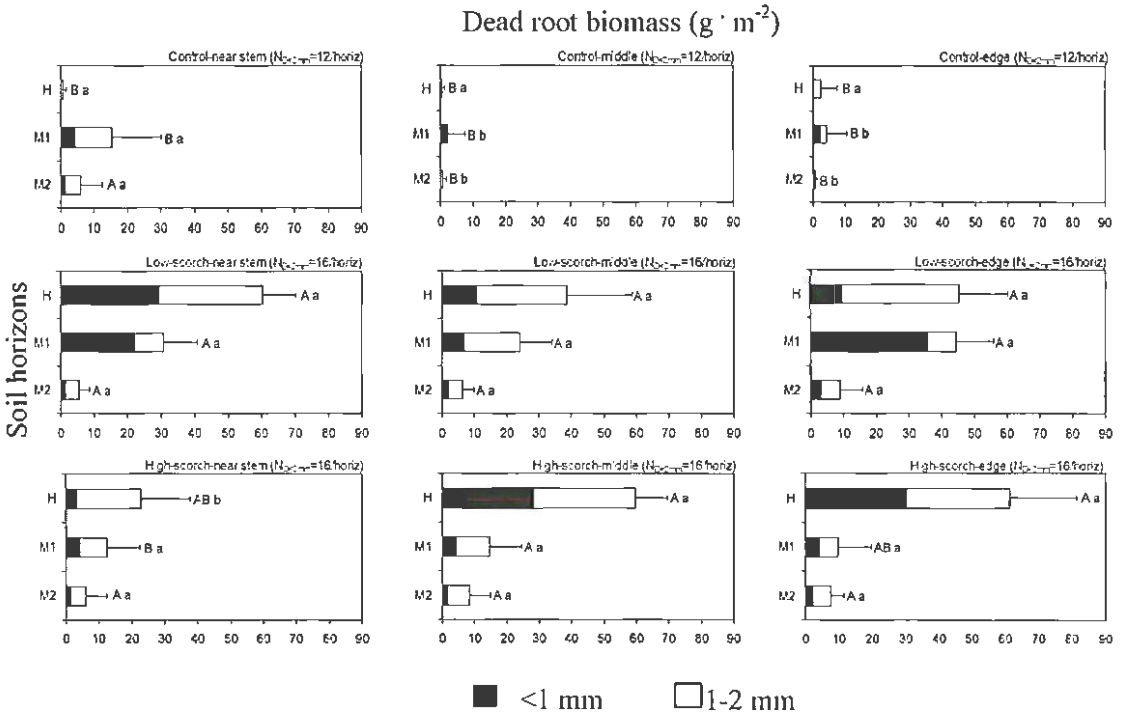

Fig. 1.3a Mean dead root biomass ($g \cdot m^{-2}$) to diameter D<2 mm. Tukey's multiple comparison tests of D<2 mm (<1 mm+2 mm) biomass rank mean among scorch classes and distances. Note: capital letters indicate differences among the corresponding distances of different scorch classes, and lower case letters indicate differences among distances within the same scorch class. Biomasses with the same letters are not significantly different. Error bars are SDs

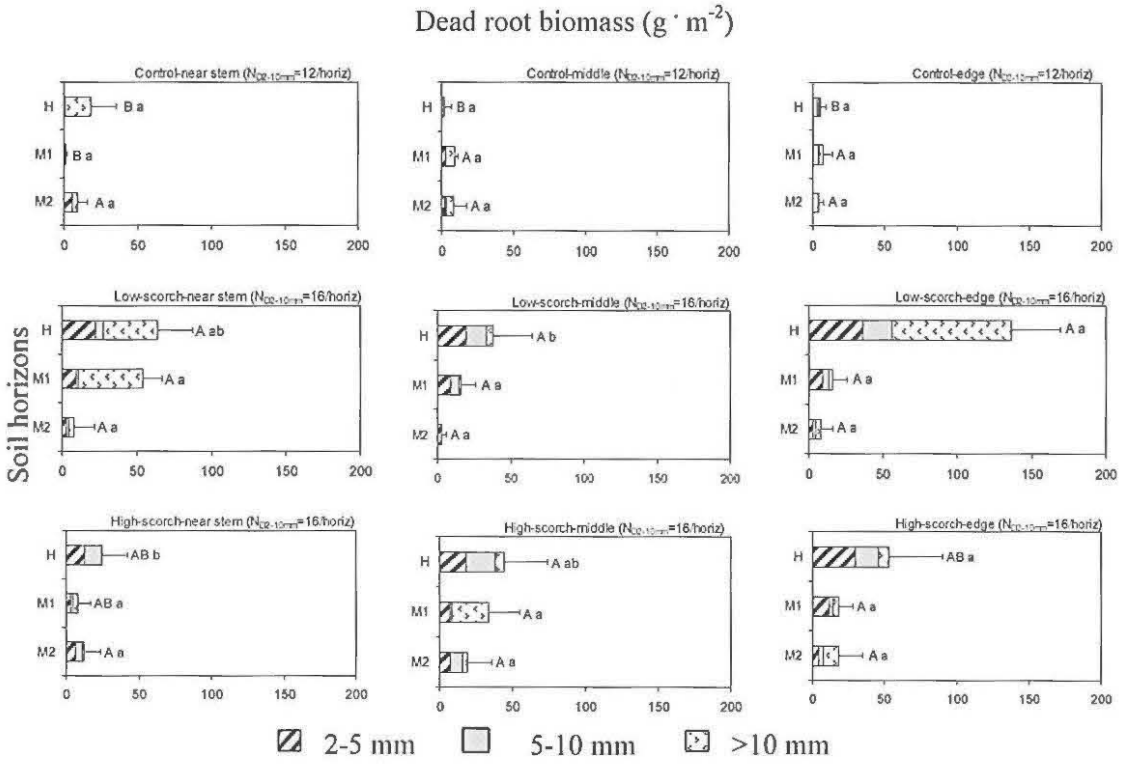

Fig. 1.3b Mean dead root biomass ($g \cdot m^{-2}$) to diameter D2-10 mm. Tukey's multiple comparison tests of D2-10 mm (2-5 mm+5-10 mm+>10 mm) biomass rank mean among scorch classes and distances. Note: capital letters indicate differences among the corresponding distances of different scorch classes, and lower case letters indicate differences among distances within the same scorch class. Biomasses with the same letters are not significantly different. Error bars are SDs

Table 1.5 Results from the ANOVA performed on ranked diameter classes of dead-root biomass

Soil horizon	Source		D<2 mm		D2-10 mm		Sum DR	
		DF	*F*	*p*	*F*	*p*	*F*	*p*
Organic horizon	Overall model	17	6.83	<0.01	3.05	0.01	5.02	<0.01
	Error	114						
	Site	1	8.04	0.01	0.93	0.34	2.31	0.13
	Scorch class	2	50.02	<0.01	14.21	<0.01	35.74	<0.01
	Distance	2	1.24	0.29	0.13	0.88	0.66	0.52
	Site*Scorch class	2	1.40	0.25	4.68	0.01	2.08	0.13
	Site*Distance	2	0.31	0.73	0.53	0.59	0.49	0.61
	Scorch class* Distance	4	8.13	<0.01	3.11	0.01	8.31	0.01
	Site*Scorch class *Distance	4	1.24	0.30	1.28	0.29	0.47	0.76
Upper mineral horizon	Overall model	17	2.67	<0.01	1.97	0.02	1.26	0.07
	Error	114						
	Site	1	0.21	0.65	4.94	0.03	2.89	0.05
	Scorch class	2	14.96	<0.01	4.24	0.02	5.76	0.02
	Distance	2	1.21	0.30	2.81	0.05	0.19	0.52
	Site * Scorch class	2	0.91	0.41	3.37	0.04	0.74	0.14
	Site * Distance	2	0.75	0.48	1.24	0.29	0.43	0.31
	Scorch class * Distance	4	7.20	0.01	2.13	0.05	0.38	0.54
	Site * Scorch class * Distance	4	0.84	0.50	1.03	0.40	0.21	0.63
Lower mineral horizon	Overall model	17	3.41	<0.01	1.16	0.13	2.22	0.01
	Error	114						
	Site	1	0.57	0.45	4.54	0.04	4.65	0.03
	Scorch class	2	19.08	<0.01	1.69	0.19	11.09	<0.01
	Distance	2	0.04	0.96	0.18	0.84	0.46	0.64
	Site * Scorch class	2	0.31	0.74	0.32	0.73	0.82	0.44
	Site * Distance	2	0.93	0.40	2.11	0.13	0.65	0.52
	Scorch class * Distance	4	2.17	0.05	1.12	0.08	0.64	0.64
	Site * Scorch class * Distance	4	1.32	0.27	1.08	0.37	0.33	0.86

1.3.4 Root production

All in-growth soil cores contained pine roots 14 months after deployment and all in-growth pine roots were less than 2 mm in diameter. In-growth root mass did not differ substantially between control and either of the scorch classes (Fig. 1.4) and there were no significant differences (Table 1.6). Root mass was similar overall for both upper and lower parts of the in-growth soil cores (Fig. 1.4). Also, there was no statistically significant difference in in-growth root mass with distance from the stem, either for the control or for the scorched trees.

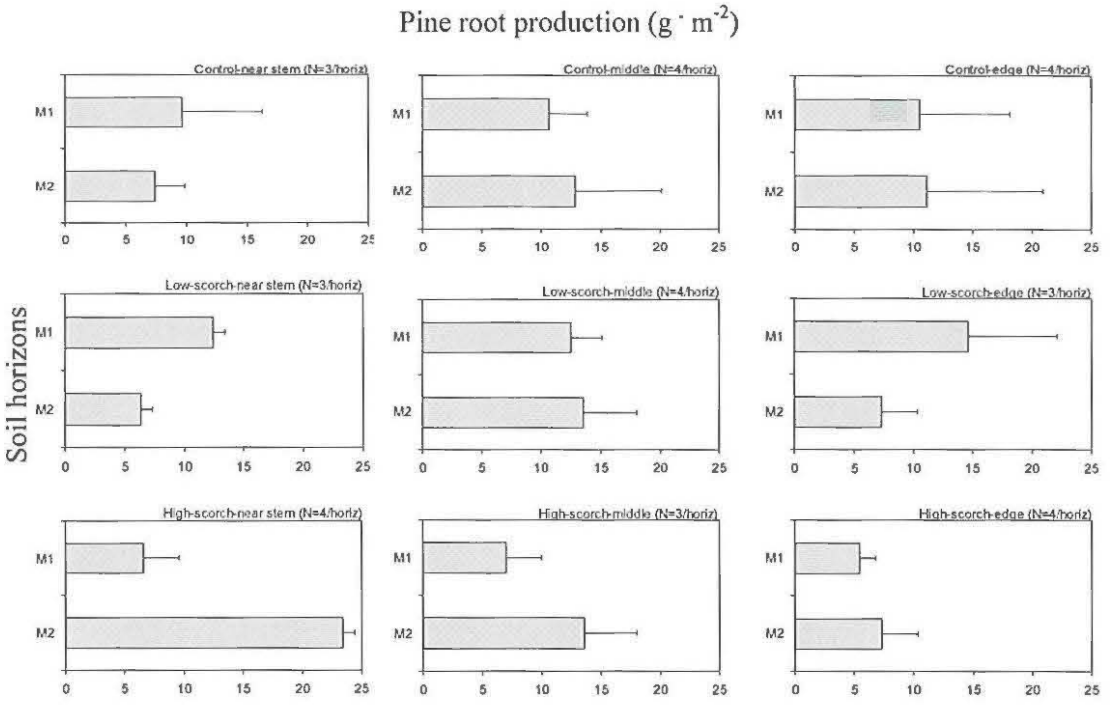

Fig. 1.4 Mean pine fine-root mass ($g \cdot m^{-2}$) in the in-growth soil cores after 14 months. Error bars are SDs

Table 1.6 Results from the ANOVA performed on pine root production

Soil horizon	Source	Production		
		DF	*F*	*p*
Upper mineral horizon	Overall model	8	0.76	0.64
	Error	22		
	Scorch class	2	1.20	0.32
	Distance	2	0.03	0.97
	Scorch class* Distance	4	0.78	2.41
Lower mineral horizon	Overall model	8	1.74	0.15
	Error	22		
	Scorch class	2	0.74	0.49
	Distance	2	0.33	0.72
	Scorch class* Distance	4	2.41	0.09

DF: Degree of freedom

1.4 Discussion

Fire had a dramatic impact on *Pinus* tree roots at these study sites. One year after fire on the burnt sites, mass of live roots with a diameter less than 2 mm in all soil horizons was on average less than 19% of that at control sites. The degree of fire-caused root death should relate to both root depth distribution and heat input into the soil, but may result from different mechanisms, such as direct heat-kill and indirect killing due to cut-off from phloem transport of girdled roots. The latter could be the main cause of death here, at least for roots in deeper soil layers, where lethal temperatures during fire are unlikely (Schimmel and Granström, 1996).

Fire intensity (*sensu* Byram, 1959) is reflected in the scorch height on the trees (Van Wagner, 1973) and thus has a direct effect on tree canopy status after fire, and ultimately on the capacity of the tree to supply roots with carbon. However, fire intensity should not have a direct influence on depth of burn, since the deeper organic layers are too compact to burn in flaming combustion (Johnson, 1992). Nevertheless, for our sample trees there was a significant relationship between scorch type and depth of burn, which makes it difficult to separate the effects of these two fire behaviour variables on post-fire root dynamics.

Deep smoldering frequently occurs beneath tree canopies (Miyanishi and Johnson, 2002), in particular close to tree stems (Miyanishi, 2001). Our observations from the excavations of fire-damaged trees suggest that the upper layer coarse roots are subjected to direct fire-girdling especially at the root collar, because there they are not covered by mineral soil. In addition, large roots that were forced by stones to grow near the surface were severely damaged. In contrast to stem bark, coarse root bark is thinner (Makkonen, 2001), thus offering little heat protection to the coarse root cambium. Indirect effects resulting from cut-off from phloem transport of girdled roots appear to have resulted in massive loss, not least for roots in deep mineral soil layers and at the edge of the canopy projection, where depth of burn was low.

Fire affected the root diameter classes differently. Thus the most severe losses were observed for the small diameter classes with diameter less than 2 mm, for all soil horizons, which is in accordance with the study by Swezy and Agee (1990).

The in-growth experiments were used as a measure of postfire root production. As photosyntate is the main source of energy for conifer root metabolism (Iivonen *et al.*, 2001; Helmisaari *et al.*, 2007) it would be expected that root production should depend on fire-damage to foliage. Surprisingly, our results from the in-growth experiment did not show any significant difference in root production between damaged and undamaged trees. This suggests a high priority for re-generating root function after fire, probably at the expense of stem growth (Sayer and Haywood 2006).

Scots pine is a moderately fire-resistant species widely distributed throughout northern Eurasia. In northern Sweden, fire-history studies have documented life-spans of several hundred years, with repeated scarring in low-intensity fires (Engelmark *et al.* 1994; Niklasson and Granström 2000). This species should be expected to be well adapted to fire, but our results nevertheless show the potential for severe root loss, mainly because of a shallow root distribution. This pattern of rooting appears to be typical for boreal soils (Persson 1993;

Taskinen *et al.* 2003) and is likely a response to the vertical distribution of nutrient release (Lindahl *et al.*, 2007)

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CHAPITRE II

STAND-REPLACING VS. NON-STAND-REPLACING FIRE IN BOREAL JACK PINE: LIVE TREES, UNDERSTORY VEGETATION AND DEAD WOOD DYNAMICS OVER TIME[1]

L'étude présentée dans ce chapitre avait pour but de vérifier l'hypothèse selon laquelle l'abondance des structures résiduelles dans les peuplements brûlés est relative au type de feu. Deux types de feux ont été évalués : les feux létaux et les feux non létaux. L'abondance et les caractéristiques des structures résiduelles suivantes : arbres vivants, bois mort et végétation de sous-bois ont été documentées et analysées. L'étude a été menée dans des peuplements de pins gris (*Pinus banksiana* Lamb.) du nord-ouest québécois.

2.0 Abstract /Résumé

North American jack pine (*Pinus banksiana* Lamb.) stands are generally characterized by an even-aged structure resulting from stand-replacing fire (SRF) of high intensity. However, non-stand-replacing fires (NSRF) of moderate intensity, which leave behind surviving trees, have also been reported. The objectives of this study were twofold: 1) assess the concurrent dynamics of live trees, understory vegetation and different types of coarse woody debris (CWD) during succession after SRF; and 2) document how NSRF affects stand structure component dynamics compared to SRF. Stands affected by both SRIF and NSRF were selected. Tree characteristics and age structure, understory biomass, and CWD volume were assessed. Our results suggest that the structural succession of jack pine stands following SRF comprises three stages: young stands (< 48 yrs), premature and mature stands (58-100 yrs), and old stands (> 118 yrs). Canopy openness and jack pine density significantly decreased with time since SRF, while black spruce density and CWD volume significantly increased. The highest structural diversity was measured in the premature and mature stands. Compared

[1]Smirnova, E., Bergeron, Y., Brais, S. 2008. "Influence of fire intensity on structure and composition of jack pine stands in the boreal forest of Quebec: live trees, understory vegetation and dead wood dynamics". Forest Ecology and Management, 225: 2916-2927.

to SRF, NSRF increased mean jack pine basal area, decreased average stand density, delayed the replacement of jack pine by black spruce replacement in the canopy, decreased CWD volume, and significantly increased bryophytes mass. NSRF increased the diversity of live trees and generally decreased CWD structural diversity. The study confirms the diversity of natural disturbance magnitude and successional processes thereby initiated. Thereafter, it appeared to be relevant for adjustment of disturbance emulating forest management systems.

Keywords: Boreal forest; Jack pine; Fire intensity; Stand structure; Black spruce; Coarse woody debris; Structural diversity

Les peuplements de pins gris (*Pinus banksiana* Lamb.) nord-américains sont généralement caractérisés par une structure d'âge équienne résultant de feux létaux (FL). Cependant, des feux non létaux (FNL) non destructeurs, laissant des arbres survivants, ont aussi été rapportés. Les objectifs de cette études sont les suivants : évaluer les dynamiques concurrentes des arbres vivants, de la végétation du sous-bois et de différents types de débris ligneux grossiers (DLG) durant la succession après un FL; et 2) documenter la façon dont les FNL affectent les dynamiques des composantes des structures de peuplements comparativement au FL. Les peuplements affectés par un FL et un FNL ont été sélectionnés. Les caractéristiques des arbres et l'âge des structures, la biomasse du sous-bois et le volume de DLG ont été analysés. Nos résultats suggèrent que la succession structurale des peuplements de pins gris après un FL comprend trois étapes : jeunes peuplements (< 48 ans), peuplements prématures et matures (58-100 ans) et vieux peuplements (> 118 ans). L'ouverture des de la voûte forestière et la densité de pins gris diminuent significativement avec le temps depuis un FL, alors que la densité d'épinettes noires et le volume de DLG augmentent significativement. La plus haute diversité structurale était mesurée dans les peuplements prématures et matures. Comparativement aux FL, les FNL augmentent la surface terrière moyenne de pins gris, diminuent la densité moyenne de peuplement, décroissent le volume de DLG et augmentent significativement la masse de bryophytes. Les FNL augmentent la diversité d'arbres vivants et diminuent généralement la diversité structurale de DLG. L'étude confirme la diversité de la magnitude des perturbations naturelles et les processus ainsi amorcés. Les résultats semblent pertinents pour un ajustement des systèmes d'aménagement forestier qui imite les perturbations naturelles.

Mots clés : forêt boréale; pins gris; intensité de feu; structure de peuplement; épinette noire; débris ligneux grossiers; diversité structurale.

2.1 Introduction

Fire intensity is defined as the energy produced by a fire event over an area during a period of time. Residual structures within a burned area can be used as an index of fire intensity for some extent (Schimmel and Granström, 1996; Turner *et al.*, 1998). North American jack pine stands are generally characterized by an even-aged, post-fire structure created by stand-replacing fires (SRF) of high intensity, in which jack pine is generally replaced by black spruce in the canopy approximately 150 yrs after the stand-initiating fire (Bergeron and Brisson, 1990; Gauthier *et al.*, 1993; Lesieur *et al.*, 2002). Although jack pine stands are generally believed to be prone to SRF, some authors (Desponts and Payette, 1992; Gauthier *et al.*, 1993) have reported the occurrence of non-stand-replacing fires (NSRF) of moderate intensity, which leave behind surviving trees, initiate a new cohort, and retain legacies from the pre-fire stands. Therefore post-fire succession of major stand structures: live trees, understory vegetation and CWD initiated by SRF and NSRF can differ.

The structural development of boreal forest stands resulted from disturbance of high magnitude can be summarized by four stages: (1) stand initiation; (2) stem exclusion with self-thinning; (3) canopy break-up, which sometimes leads to the initiation of a new cohort (although not in fire-dependent jack pine); and (4) old growth, characterized by high structural diversity (Oliver, 1981; Kenkel *et al.*, 1997; Boucher *et al.*, 2006).

Functional traits are considered to be a useful tool to understand plant responses to different disturbance characteristics (Schoennagel *et al.*, 2004). The understory composition of jack pine boreal stands can be divided into four functional groups (De Grandpré *et al.*, 1993): dwarf ericaceous shrubs, herbs, bryophytes, and lichens. Secondary succession in the understory layer starts with pioneer species such as lichens and herbs (MacLean and Wein, 1977; Nguyen-Xuan *et al.*, 2000). However often most understory species survive fire via buried rhizomes and re-establish quickly after fire, before canopy closure (Schimmel and Granström, 1996). Understory vegetation in old jack pine stands varies from bryophytes

(including *Sphagnum* spp.) to lichens depending on site drainage and stand density (Foster, 1985; Béland and Bergeron, 1996; Fenton and Bergeron, 2006; Lecomte *et al.*, 2006).

In several types of boreal stands, CWD dynamics is characterized by a "U-shaped" temporal pattern (Harmon *et al.*, 1986; Sturtevant *et al.*, 1997; Brais *et al.*, 2005; Harper *et al.*, 2005). The early stage of forest development is characterized by relatively high amounts of CWD generated before the disturbance or as a result of it. During the first years after disturbance, self-thinning process also generates debris; their amount is related to stand history (Spies *et al.*, 1988; Hély *et al.*, 2000). Further, debris amount declines with time, with little input from regenerating sages (Sturtevant *et al.*, 1997; Kenkel *et al.*, 1997). CWD input peaks during the transitional stage, when even-aged mature stands senesce and shift to an uneven-aged structure (Sturtevant *et al.*, 1997; Harper *et al.*, 2005).

NSRF can alter structural diversity, as well as the timing and amplitude of stand developmental stages (McRae *et al.*, 2001). NSRF result in a decrease of self-thinning and subsequent growth release (Rothstein *et al.*, 2004; Weisberg, 2004), the initiation of a new jack pine cohort (Bergeron and Brisson, 1993; Gauthier *et al.*, 1993), and changes in species composition, as NSRF kills the seedlings and young individuals of late successional species, such as black spruce and balsam fir (Weisberg, 2004). Furthermore, changes in live tree structure induced by NSRF may eventually alter CWD dynamics.

Fire behaviour depends on multiple factors: weather conditions, topography, fuel characteristics such as their amount and moisture content (Nelson, 2001; Sandberg *et al.*, 2007). Fire intensity as measured by scorch height (*sensu* Byram, 1959) does not relate directly to fire severity at the ground level because different processes are involved i.e. different phases of combustion vs. pyrolis (Johnson, 1992).

The diversity of natural disturbance magnitude represents a particular interest for disturbance emulating forest management (McRae *et al.*, 2001). Variable tree-retention

systems permits to emulate non-stand-replacing fires in jack pine stands; at present the information of successional process in jack pine stands survived NSRF is largely missing.

Although a few authors have already described jack pine stand development after SRF (Gauthier *et al.*, 1993; Béland *et al.*, 2003; Hamel *et al.*, 2004; Lecomte and Bergeron, 2005), there has been few study dedicated to the influence of NSRF on jack pine stand structural development (Gauthier *et al.*, 1993; 1996; Gagnon, 1990). The objectives of this study were: 1) to assess the concurrent dynamics and structural diversity of live trees, CWD and understory vegetation during succession after SRF; and 2) to document how NSRF alters the dynamics and diversity of these structural components.

The hypotheses of the study are: 1) NSRF provides a rejuvenating effect on stand structure by delaying stand senescence; 2) NSRF increases stand structural diversity compared to SRF.

2.2 Study area

The study area is located in northwestern Quebec (Fig. 2.1; Table 2.1; Appendice A), in the southeastern Canadian boreal forest. The climate is continental, characterized by a mean annual temperature of 0.7 ^{o}C and 890 mm of precipitation (Environment Canada, 2004). While the area is part of the Precambrian Shield, Quaternary surface deposits cover most of the territory and the soils of our study sites have evolved from coarse-textured glaciolacustrine deposits (Brais and Camiré, 1992).

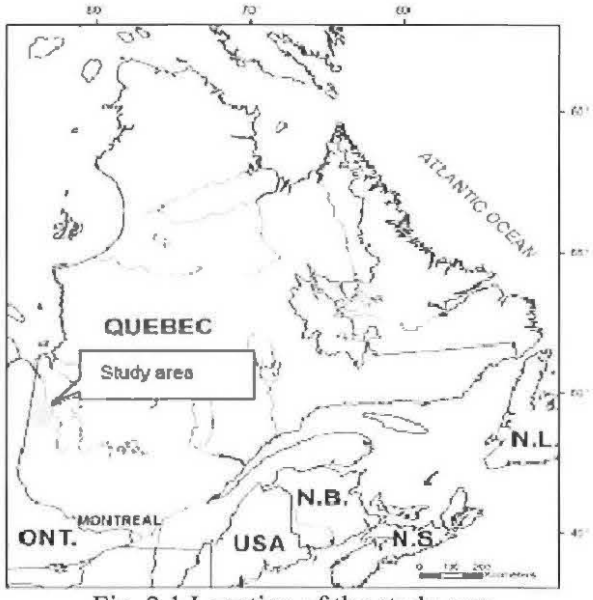


Fig. 2.1 Location of the study area.

Table 2.1 Description of the study sites

Site	Year of SRF/ time since SRF (yrs)	Year of NSRF/ time since NSRF (yrs)	Stand age when NSRF occurred (yrs)	Scarred jack pine live trees (%)	Scarred snags (%)	Stand groups
H1	1979 / 23					I
H2	1969 / 33					I
H3	1955 / 48					I
H4	1945 / 58					II
H5	1934 / 69					II
H6	1927 / 76					II
H7	1918 / 85					II
H8	1903 / 100					II
H9	1885 / 118					III
H10	1854 / 149					III
H11	1848 / 155					III
M1	1927 / 77	1950 / 53	23	13.26	59.13	IV
M2	1920 / 83	1951 / 52	31	8.80	3.03	IV
M3	1916 / 87	1970 / 33	54	12.22	16.67	IV
M4	1909 / 94	1951 / 53	42	5.93	23.23	IV
M5	1908 / 95	1973 / 30	65	5.83	26.67	IV
M6	1863 / 143	1917 / 86	54	15.39	30.95	V
M7	1850 / 154	1916 / 87	66	4.88	22.92	V
M8	1850 / 154	1917 / 86	67	13.62	11.11	V

2.3 Methods

2.3.1 Stand selection

Eleven post-SRF jack pine stands were selected along a chronosequence (SRF stands). The selected stands varied in size from ca. 10 to 20 ha and showed no trace of forestry practices. Nicolas Lecomte (Lecomte *et al.*, 2006) provided the data for two of the stands (H10 and H11: 149 and 155 yrs after SRF). Evidence that stands originated after a SRF was based on the absence of fire-scarred trees, an even-aged stand structure, and the absence of evidence of forest-management operations, such as stumps or regular tree distribution. The fire year for each stand was estimated by determining the age of the oldest canopy tree (Lesieur *et al.*, 2002). Within or close to SRF stands, eight stands were selected that also survived a moderate intensity fire (NSRF stands). Stand size varied from 0.5 to ca. 7 ha. Characteristic fire scar (Gutsell and Johnson, 1996) at the base of the tree provided evidence for NSRF occurrence. At least ten jack pine trees were sampled (cores) in each SRF stand for stand age determination. For NSRF stands, samples were taken from 1-4 scarred trees (discs) and at least ten non-scarred trees (cores) for stand age determination. Furthermore, the distribution of scarred trees was used to delineate the spatial extent of NSRF.

2.3.2 Live tree measurements

In each SRF and NSRF stand, five circular plots with a radius of 8 m and separated by 50 m were established. The circles formed a box with plots at each corner with one circle in the middle. Tree taxon, live tree status and presence of fire scars were also noted. Live tree status was based on the classification used by Imbeau and Desrochers (2002): (1) alive and healthy, with more than 95% foliage; (2) 20 to 95% foliage remaining; and (3) dying, with less than 20% foliage remaining. Diameter at breast height (DBH) was measured for all trees, and standing dead trees (snags) were measured (height) and dated.

Fisheye photographs were taken with a Nikon Coolpix 990 camera, (version 6.0) furnished by *fisheye* objective (Nikon FC-E8) above high shrub canopy (3 m height) in five replications per circular plot: north, south, east, west, and centre. The photographs were taken during uniform overcast days. The photographs were treated by Gap Light Analyzer (Frazer *et al.*, 1999) package and analyzed with Adobe Photoshop software (v. 8) to yield a percentage of open sky seen from beneath the canopy. Canopy openness data was not available for SRF stands H10 and H11.

2.3.3 Dead wood measurements

Tree taxon, decomposition class and presence of fire scars were documented. Snags decay stages were classified according to Imbeau and Desrochers (2002): (1) recently dead tree with sound wood and bark but no green foliage; (2) sound wood, no foliage; (3) sound wood, no bark, broken top, but more than 50% of the height of a live tree of comparable DBH; (4) decomposed wood, broken top, height less than 50% that of a live tree of comparable DBH; and (5) stump, height less than 2 m. DBH was measured for snags and stumps (diameter at the top of the stump was used for stumps < 1.3 m).

Downed wood volume (logs) was assessed by diameter and decomposition class along six 50 m-transects systematically established around the five circle plots and connecting their centres (300 m in total). Log decomposition class was identified according to the five-class system described by Thomas et al. (1979), based on the structural characteristics of the boles: (1) sound bark and wood, presence of twigs; (2) branches present, bark mostly intact, (3) bark detached or absent, vegetation covering the log; (4): log oval, bark absent, wood soften due to decay; and (5) structural integrity lost and log incorporated into the forest floor.

2.3.4 Understory vegetation

Biomass measurements were taken in order to assess the effects of different fire intensities on the dynamics of understory functional groups. Dominant functional groups were identified according to a visual estimation of the dominant species (Table 2.2). The aboveground understory biomass was sampled within four quadrants (0.5 m^2) established 4 m from the centre of each plot in the four cardinal points (North, South, East, and West). Biomass was sampled in the field; subsample of plants of each functional group was brought to the laboratory to identify the loss of ignition weight. Understory biomass data were not available for SRF stands H10 and H11.

Table 2.2 Dominant species for each functional group of understory vegetation

Ericaceous shrubs
Vaccinium angustifolium, Ait.
Vaccinium myrtilloides, Michx.
Kalmia angustifolia, L.
Epigea repens, L.
Gaultheria procumbens, L.
Gaultheria hispidula, (L.) Muhl.
Rhododendron groenlandicum, Oeder.
Herbs
Linnaea borealis, L.
Aralia nudicaulis, L.
Pyrola secunda, L.
Clintonia borealis, Raf.
Trientalis borealis, Raf.
Cornus canadensis, L.
Coptis groenlandica, (Oeder.). Fern.
Bryophytes
Polytrichum spp.
Pleurozium schreberi, (Brid.) Mitt.
*Hylocomium splendens, (*Hedw.) Schimp.
Dicranum spp.
Lichens
Cladonia spp.
Cladina spp.

2.3.5 Laboratory methods

CWD field measurements were transformed into volume. For snag volume, the truncated cone equation (Rondeux, 1993) was used:

$$V_{snags} = \pi Hs^2/12(D^2+d^2+Dd)^2. \quad (1)$$

where Hs is snag height, D is snag diameter at the base, and d is diameter at the top of the snag. These dimensions were derived from the proportions:

$$D=Ht \times dbh/Ht-1.3, \text{ and } d=D\ (Ht-Hs)/Ht, \quad (2, 3)$$

where Ht is tree height before breakdown, which was calculated based on the Chapman-Richards equation:

$$Ht = (130+B_0(1-e^{-B_1 dbh}))^{B_2}/100 \quad (4)$$

The equation operates with a set of coefficients (B_0, B_1, B_2) specific for different ecological regions of jack pine growth (Brais *et al.*, 2005).

For log volume, the following equation was applied (Van Wagner, 1978):

$$V_{logs} = (5.234/L) \times density \times d^2. \quad (5)$$

where L is transect length, d is log diameter, and density is the number of logs per transect.

For understory biomass calculations, ten samples of each functional group (bryophytes, lichens, ericaceous shrubs and herbs) per stand were oven dried after its fresh biomass was corrected for moisture content.

2.3.6 Statistical analyses

Regression analysis was used to find the relationship between response variables and time since fire for SRF stands. The influence of observations by means of Cook's was evaluated. Thus, if an observation was an outlier based on Cook's distance, it has been removed from the analyses.

Since NSRF stands did not form a chronosequence comparable to the chronosequence of SRF stands, the hypothesis of a rejuvenating effect of NSRF on stand structure was tested using a canonical discriminant analysis to assess the relationships between major stand structure variables (canopy openness, jack pine and black spruce basal area and density, snag and log volume, and understory biomass) among SRF and NSRF stands. This analysis indicated the stand structure variable that contributed the most to discrimination among stands. Stands that were affected by the same stand structure variables were grouped, and Mahalanobis distance analysis was used to assess the significance of the difference between groups. Finally, we used a discriminant analysis to find the difference of each structure among *a priori* groups of corresponding time since SRF. Therefore young stands resulted from SRF were not compared to NSRF stands. The analyses were done with stands replicated with sub-samples of circular sampling plots.

To determine the influence of fire intensity on structural diversity, *alpha* diversity and *beta* diversity were calculated for major stand structure variables within SRF and NSRF stands and along the chronosequence. The *alpha* diversity of live jack pine was defined as the number and abundance of DBH classes. For snags, it was defined as the number and

abundance of DBH classes in each decomposition class. The Shannon-Wiener index (H) was used to calculate *alpha* diversity:

$$H = -\Sigma\, p_i \ln p_i \quad (6)$$

where p_i is the relative importance of a DBH class (Scherrer, 1984).

Sorensen's index of similarity was used to assess the *beta* diversity of understory vegetation functional groups:

$$S = c/\alpha \quad (7)$$

where c is the number of species common to each pair of plots, and α is the average number of understory functional groups found within each plot (Vellend, 2001). All possible pairs of plots were tested. Afterwards, discriminant analysis was used to evaluate the difference in structural diversity coefficients among SRF and NSRF groups of corresponding time since SRF.

Data analyses were completed with the SAS statistical package (SAS Institute Inc., 1985).

2.4 Results

2.4.1 Stand dating

The youngest and oldest SRF stands established 23 yrs and 155 yrs after fire, respectively (Table 2.1). Stands that survived NSRF can be characterized in three ways, according to: 1) time since stand-replacing SRF, 2) time since NSRF, and 3) age of stands at the moment when NSRF occurred. Time since stand-replacing SRF ranged from 77 to 154 yrs. Based on

time since NSRF, the stands can be divided into three groups: those recently affected by NSRF (30 and 33 yrs since NSRF), intermediate age NSRF (52 and 53 yrs since NSRF) and old NSRF (86 and 87 yrs since NSRF). NSRF occurred between 23 and 68 yrs after stand-replacing SRF, i.e. before stand maturity.

In NSRF stands, tree-core assessment indicated the general age evenness of jack pines. Fire-scarred jack pines were found within each circular plot, although the number of scarred and non-scarred live trees and snags (Table 2.1) differed between stands. The highest number of scarred live trees and snags was measured in the youngest stand (IV) that was 23 yrs when NSRF occurred.

2.4.2 Stand grouping

Three axes among six axes identified by the canonical discriminant analyses were significant (Table 2.3). Most stand structure variables were significantly correlated with the first three canonical axes (Table 2.4).

Table 2.3 Canonical discriminant analysis for structural association that generated five SRF and NSRF stand groups

	Eigenvalue	Contribution %	F	*p*
CAN I	8.95	65.26	19.76	<.01
CAN II	4.10	29.85	11.27	<.01
CAN III	0.59	4.07	3.81	<.01

Table 2.4 Correlation of canonical axes with stand structure variables

	CAN I	CAN II	CAN III
Canopy openness	-0.60***	0.08	-.42***
JP[1] total density	0.18***	0.90***	0.27
BS[2] total density	0.97***	-0.14	-0.03
JP basal area	-0.05	-0.50***	0.29**
BS basal area	0.44***	-0.57***	-0.12
Total snag volume	0.32**	-0.09	0.80***
Total log volume	0.20*	-0.41***	0.15*
Total understory	-0.35**	-0.41***	-0.19

[1]JP - Jack pine; [2] BS - Black spruce *$p < .05$; **$p < .01$; ***$p < .001$

CWD volume of SRF stands of 23 and 33 yrs were not included in the analysis because of the outstandingly low CWD volume in these stands; which is controversial to the literature sources that reported high CWD volume in postdisturbance stands (Harmon *et al.*, 1986; Sturtevant *et al.*, 1997). The canonical discriminant analysis ordination diagram allowed to separate SRF stands into three groups (Fig. 2.2; Table 2.5): young stands (group I, 23-48 yrs), premature and mature stands (group II, 58-100 yrs), and old stands (group III, 118-155 yrs). NSRF stands were less easily divided into groups but nevertheless separated between younger (group IV, 77-95 yrs) and older (group V 143-154 yrs).

Table 2.5 Distinction between SRF and NSRF stand groups according to Mahalanobis squared distance (F) and the associated probability.

Stand groups	I	II	III	IV	V
I	0				
II	6.32,<.01	0			
III	56.44,<.01	61.24,<.01	0		
IV	26.18,<.01	24.36,<.01	73.17,<.01	0	
V	14.97,<.01	12.02,<.04	57.44, <.01	2.80, <.05	0

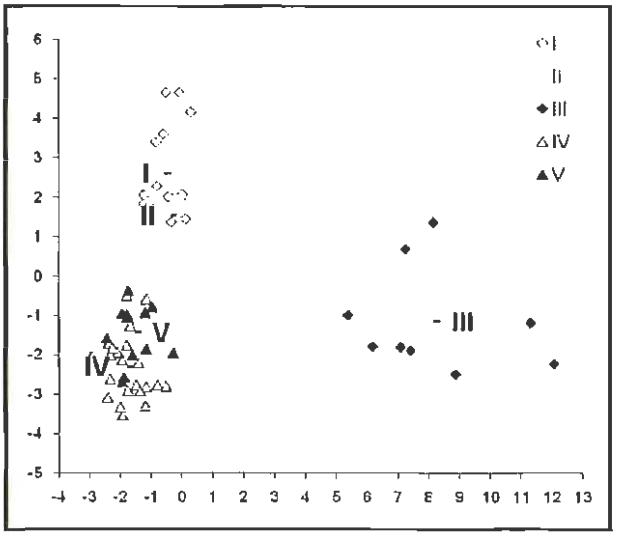


Fig. 2.2 First and second canonical axes generated by canonical discriminant analysis of stands associations in five groups. Means are indicated for each group (I to V).

2.4.3 Live trees

Live tree stem density and basal area

In SRF stands, canopy openness linearly decreased with time since SRF (Fig. 2.3; Table 2.6). The relationship between canopy openness and time since SRF is significant, when an outlier (85 yr SRF stand) identified by Cook's distance analysis, has been removed. Mean total jack pine basal area followed a linear trend with time SRF; while black spruce basal area significantly increased with time since SRF (Table 2.6; Figs. 2.4 a, b). Jack pine small and intermediate stem density decreased with time since SRF, while density of large sized jack pine stems increased (Table 2.6, Fig. 2.5 a). Black spruce density increased with time since SRF (Fig. 2.5 b).

Discriminant analysis indicated that only jack pine and black spruce basal area and large diameter jack pine density differed significantly between NSRF stand groups (Table 2.6). Jack pine and black spruce basal areas in NSRF stands were significantly inferior compared to the groups II and III of SRF stands; meanwhile big-diameter jack pine density was higher in NSRF stands. NSRF resulted in higher canopy openness and significant decrease in black spruce density compared to old SRF stands (group H3).

Compared to SRF, NSRF significantly increased canopy openness in younger and older stands (groups II and III vs. IV and V) (Fig. 2.3; Table 2.6). NSRF also significantly reduced black spruce basal area and density in both younger and older stands (Figs. 2.4, 2.5; Table 2.6). NSRF significantly decreased small diameter jack pine basal area in younger stands, and increased the density of large diameter jack pines in older stands (Table 2.6).

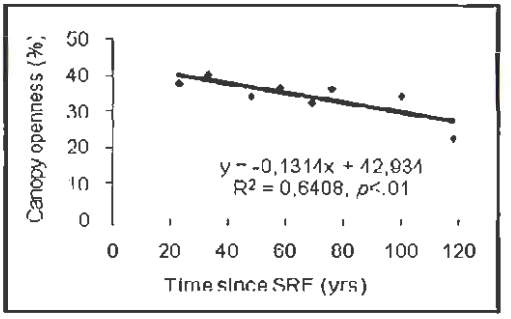
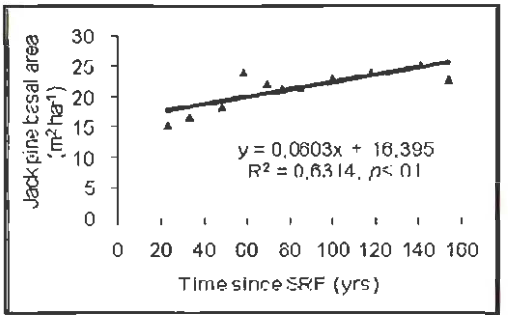


Fig. 2.3 Canopy openness according to time since stand replacing fire, SRF stands (♦).



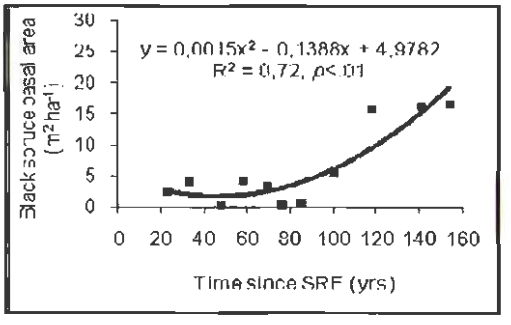
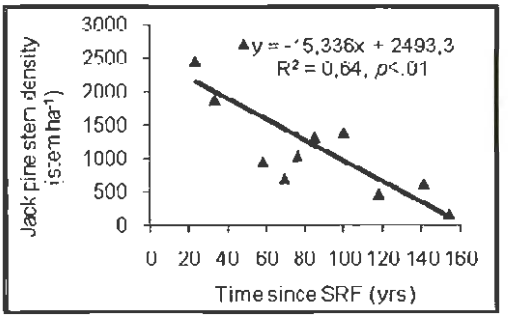


Fig. 2.4: a) Jack pine basal area according to time since fire in SRF stands (▲); b) black spruce basal area according to time since fire in SRF stands (■).



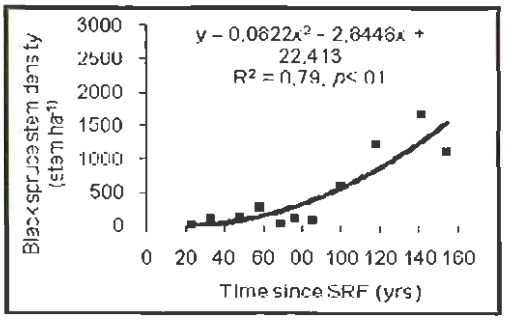


Fig. 2.5 a) Jack pine density in SRF stands (▲); b) black spruce density according to time since fire in SRF stands (■).

2.4.4 Coarse woody debris

Snags

In SRF stands, mean total CWD volume (snags with logs) followed a polynomial trend (second order) as a function of time since fire (R^2=0.66, $p < 0.04$) (*trend not shown*). Stands of 23 and 33 yrs originated from SRF have been removed from the relationship. Snag volume significantly increased along the chronosequence (Fig. 2.6 a). Small and intermediate diameter snag volume differed significantly between older SRF stand groups (Table 2.6).

In NSRF stands only large diameter snag volume differed significantly between groups (Table 2.6). Mean total snag volume of both NSRF stand groups was significantly lower compared to SRF stand groups of comparable age (Table 2.6). NSRF significantly decreased small and intermediate-diameter snag volume and increased, large-diameter snag volume compared to SRF stands (Table 2.6).

Table 2.6 Mean values (with standard deviation) of the stand structure variables and structural diversity indices for stand groups I-V. Mahalanobis distance probability indicates significant differences between stand groups. Statistically significant differences are indicated with boldface characters.

Variable	Mean values (std) per stand association					Mahalanobis distance probability (p)					
	I n=15	II n=25	III[3] n=8	IV n=22	V n=13	I vs. II	I vs . III	II vs. III	IV vs. V	IIvs. IV	III vs. V
Openness	37.42 (4.4)	26.85 (7.6)	22.62 (9.8)	32.84 (5.5)	35.48 (8.2)	**.03**	**.01**	.09	.22	**.05**	**<.01**
Total JP basal area, m^2/ha	16.19 (7.1)	22.45 (3.4)	24.11 (6.25)	29.35 (8.4)	17.15 (8.7)	**.02**	**.02**	.54	**<.01**	**.01**	**.05**
Total BS basal area, m^2/ha	2.11 (1.9)	2.65 (2.3)	19.10 (5.7)	1.85 (3.0)	10.89 (10.5)	.86	**<.01**	**<.01**	**.03**	**<.01**	**<.01**
JP[1] total density, stem/ha	2340.67 (431.5)	1064.0 (283.2)	401.67 (229.7)	847.20 (385.5)	844.67 (465.39)	**.01**	**<.01**	**<.01**	.99	**.01**	**.01**
JP 5-9 cm density, stem/ha	1170.00 (236.4)	181.80 (162.7)	36.67 (32.15)	124.30 (145.74)	195.00 (189.9)	**<.01**	**<.01**	.25	.56	.59	.27
JP 11-17 cm density, stem/ha	1025.00 (168.0)	658.00 (387.7)	123.33 (125.0)	352.50 (235.6)	488.67 (288.9)	.09	**.01**	**.02**	.51	.10	.13
JP 19-27cm density, stem/ha	145.67 (252.3)	224.20 (178.2)	241.67 (80.4)	330.40 (188.8)	157.67 (143.5)	.56	.52	.90	.21	.37	.58
JP > 27cm density, stem/ha	0.00	0.00	0.00	40.00 (41.8)	3.33 (5.8)	nd	nd	nd	**.04**	**<.01**	**.05**
BS[2] total density, stem/ha	266.00 (348.6)	213.00 (229.3)	1306.67 (261.0)	466.20 (457.8)	381.67 (432.8)	.84	**.01**	**.01**	.75	.28	**.01**
BS 5-9 cm density, stem/ha	238.33 (301.4)	143.80 (157.4)	476.67 (68.1)	266.80 (247.6)	200.67 (168.5)	.54	.18	**.04**	.67	.36	.12
BS 11-17cm density, stem/ha	27.67 (47.9)	69.20 (75.8)	730.00 (323.6)	181.20 (261.8)	174.33 (256.1)	.79	**.01**	**.01**	.97	.42	**.01**
BS 19-27cm density, stem/ha	0.00	0.00	100.00 (11.3)	18.20 (29.6)	6.67 (11.6)	nd	**<.01**	**<.01**	.35	.10	**<.01**

[1]JP –jack pine; [2] BS-Black spruce; [3]Canopy openness, understory vegetation biomass, understory vegetation structural diversity in stand group H3 were measured in only one stand (H10); for these variables n=5

Table 2.6 (cont)

Variable	Mean values (std) per stand association					Mahalanobis distance probability (p)					
	I n=15	II n=25	III[3] n=8	IV n=22	V n=13	I vs. II	I vs. III	II vs. III	IV vs. V	IIvs. IV	III vs. V
Total snag volume, m^3/ha	nd	76.07 (37.5)	117.75 (77.9)	40.11 (23.0)	39.51 (9.2)	nd	nd	.30	.79	**.02**	**.01**
Snags 5-9 cm volume, m^3/ha	nd	22.86 (18.8)	6.76 (5.12)	8.76 (7.1)	12.47 (2.6)	nd	nd	**.01**	.51	**.01**	.26
Snags 11-17cm volume, m^3/ha	nd	35.3 (18.4)	20.79 (16.3)	17.82 (9.8)	12.37 (9.9)	nd	nd	**.03**	.24	**.01**	.46
Snags 19-27cm volume, m^3/ha	nd	16.81 (23.4)	87.79 (77.1)	13.54 (9.9)	9.20 (7.8)	nd	nd	**<.01**	.69	.73	**<.01**
Snags > 27 cm volume, m^3/ha	nd	1.08 (2.42)	2.42 (4.19)	0.00	5.48 (4.9)	nd	nd	.26	**.03**	.58	.67
Total log volume, m^3/ha	nd	16.06 (6.4)	34.68 (5.3)	18.13 (8.9)	25.89 (14.1)	nd	nd	**.02**	.32	.49	.12
Logs 5-9 cm volume, m^3/ha	nd	4.81 (0.9)	1.64 (2.2)	4.30 (3.9)	5.18 (1.6)	nd	nd	.29	.85	.77	.54
Logs 11-17cm volume, m^3/ha	nd	7.65 (4.6)	7.25 (2.4)	6.25 (3.4)	7.95 (2.1)	nd	nd	.88	.72	.83	.98
Logs 19-27cm volume, m^3/ha	nd	3.33 (2.6)	22.56 (5.9)	4.07 (3.4)	6.79 (6.3)	nd	nd	**<.01**	.44	.68	**<.01**
Logs > 27cm volume, m^3/ha	nd	0.27 (0.6)	3.24 (5.6)	3.51 (3.9)	5.98 (5.5)	nd	nd	.08	.31	.34	.89
Total understory biomass, kg/ha	463.09 (122.42)	535.77 (174.8)	273.18 (135.4)	766.19 (261.4)	966.14 (454.9)	.56	.20	.37	.22	**<.01**	**.01**
Bryophytes biomass, kg/ha	230.26 (164.1)	259.27 (170.14)	207.55 (152.6)	549.90 (340.6)	691.64 (400.3)	.69	.94	.80	.11	**<.01**	.21
Ericaceae biomass, kg/ha	211.60 (73.2)	190.44 (137.6)	61.86 (54.2)	158.37 (117.7)	88.75 (45.1)	.33	**.01**	**.05**	.34	.65	.50
Lichens biomass, kg/ha	12.59 (18.93)	76.37 (86.7)	3.25 (2.8)	48.82 (99.3)	185.76 (145.8)	.37	.80	.30	**.01**	.94	**.01**
Herbs biomass, kg/ha	8.46 (2.9)	9.70 (9.6)	0.51 (0.4)	9.11 (10.1)	0.00	.96	.06	**.05**	**.01**	.63	**.91**

Table 2.6 (cont)

Variables	Mean values (std) per stand association					Mahalanobis distance probability (p)					
	I n=15	II n=25	III[3] n=8	IV n=22	V n=13	I vs. II	I vs. III	II vs. III	IV vs. V	IIvs. IV	III vs. V
diversity of live trees and CWD (Shannon-Wiener index), understory functional group beta diversity (Sørenson's index).											
Live trees	1.53	1.53	1.03	1.74	1.42	.96	**.01**	**<.01**	**.05**	.13	**.04**
Snags	nd	2.82	2.19	1.63	1.63	nd	nd	.18	.99	**<.01**	.29
Logs	nd	1.11	1.77	1.23	1.36	nd	nd	**.01**	.61	.56	.14
Understory functional groups	0.65	0.70	0.50	0.63	0.43	.56	.20	**.05**	.06	.37	.55

Logs

In SRF stands, log volume significantly increased with time since fire (Table 2.6, Fig. 2.6 b). Mean total log volume in NSRF stands did not differ significantly among groups IV and V (Table 2.6; Fig. 2.6 b). Only the volume of large diameter logs differed significantly between old SRF and NSRF stands (Table 2.6).

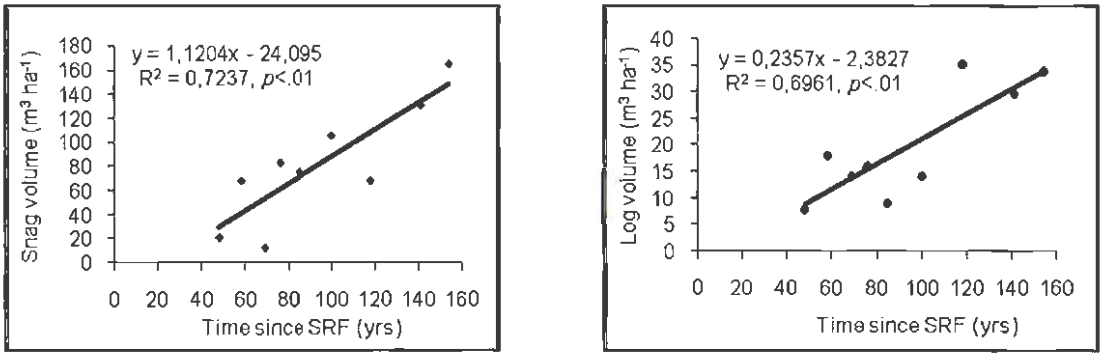


Fig. 2.6: a) Snag volume according to time since stand-replacing fire in SRF stands (♦); b) log volume according to time since stand-replacing fire in SRF stands (●).

2.4.5 Understory vegetation

Total understory vegetation biomass in SRF stands followed an S-shaped trend with time since SRF (Fig. 2.7 a) characterized by two peaks (H2, H7) and two depressions (H4, H9). Only ericaceous biomass changed (decreased) significantly with time since SRF (Table 2.6). Understory biomass in NSRF stands was significantly higher than in SRF stands (Table 2.6, Fig. 2.7 b).

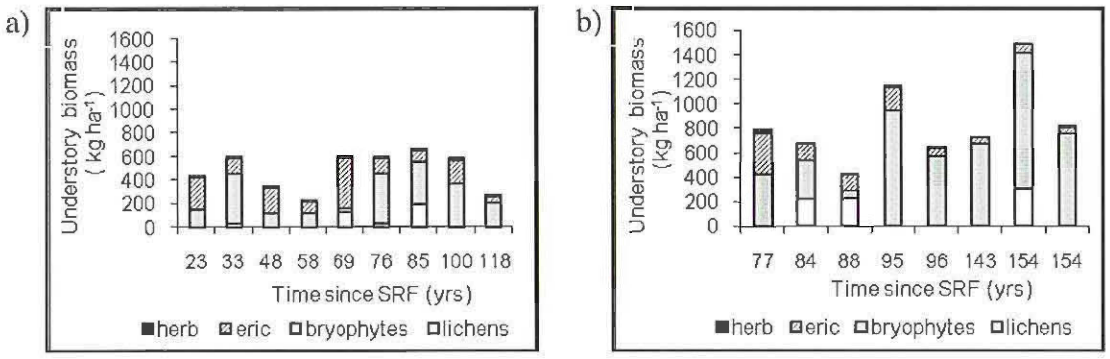


Fig. 2.7 Understory biomass in SRF stands (a) and understory biomass in NSRF stands (b).

2.4.6 Structural diversity

Jack pine live tree diversity decreased with time since fire in SRF stands (Fig. 2.8 a), but differed only weakly between NSRF stand groups (Table 2.6, Fig. 2.8 a). Jack pine live tree diversity was significantly higher in the old NSRF stands than in the old SRF stands (Table 2.6).

Snag structural diversity in SRF stands followed a linear trend with time since fire (Fig. 2.8 b). NSRF significantly decreased snag structural diversity in younger stands (Table 2.6).

In SRF stands, log diversity increased with time since fire (Fig. 2.8 c). In contrast, log diversity in all NSRF groups was similar (Table 2.6). NSRF did not significantly affect log diversity (Table 2.6).

In SRF stands, understory vegetation *beta* diversity (Sørenson's index of similarity) did not vary significantly with time since SRF (Fig. 2.8 d) and was similar in NSRF and SRF stands of comparable age (Table 2.6).

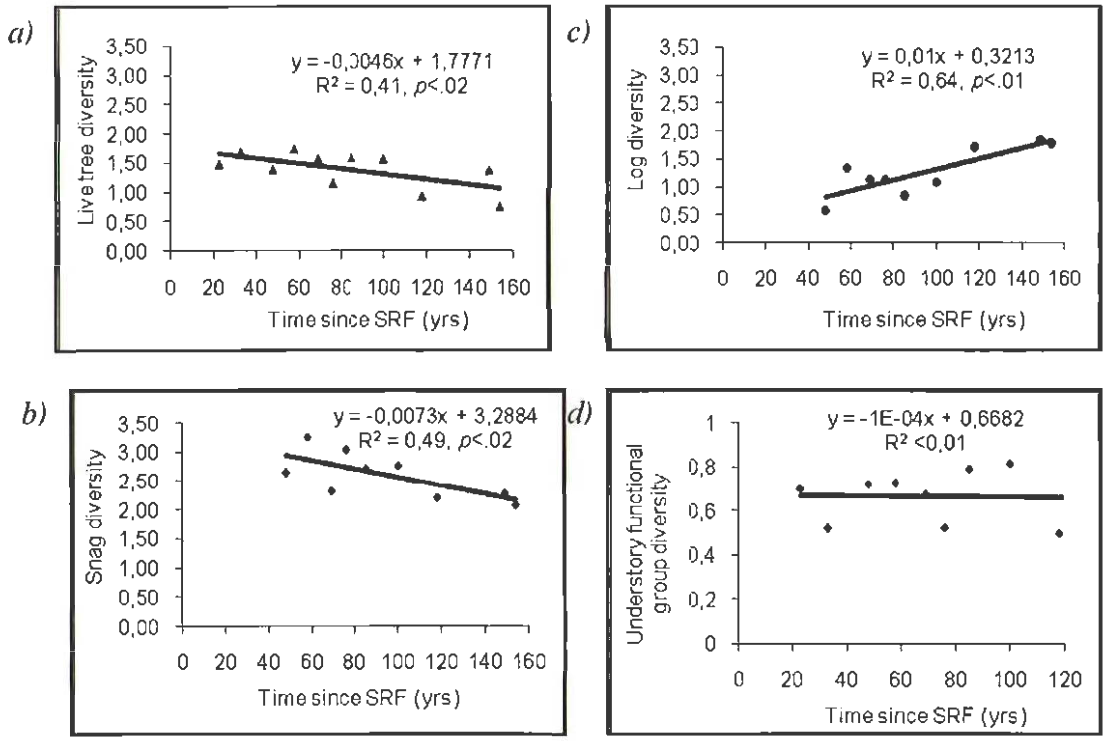


Fig. 2.8 Changes of Shannon index of structural diversity with time since stand-replacing fire in SRF stands: a) live jack pines (▲); b) snags (♦); c) logs (●); c) Sørenson's index of understory functional group diversity (♦).

2.5 Discussion

2.5.1 Jack pine stand structure development following stand-replacing fire

Average jack pine basal area (21.4 m^2/ha) and density (1231.6 stem/ha) obtained for SRF stands in this study were within the range of previously published results (Gauthier *et al.*, 1993; Béland *et al.*, 2003; Lecomte *et al.*, 2006). The range of CWD volume obtained in this study (0.6 – 221.0 m^3/ha) was wider than those reported by Brais *et al.* (2005) for jack pine stands of north-western Quebec (16.1 - 113.0 m^3/ha) and Sturtevant et al. (1997) for balsam fir and mixed fir-black spruce forests in Newfoundland (15.2 - 78.1 m^3/ha). This was likely to be so because the considered time gradient was longer in our study, compared to previous

ones. Understory vegetation biomass (average 444.3 kg/ha) changes along the chronosequence were comparable to what was reported by Lecomte and Bergeron (2005).

Based on stand structure analysis, the post-SRF succession can be divided into three stages: young stands (< 48 yrs); premature and mature stands (58-100 yrs), and old stands (> 118 yrs).

Young SRF Stands (< 48 yrs)

The dense monospecific structure of young stands is a result of quick and effective post-fire jack pine recruitment. The amount of CWD during the stand establishment stage depends on individual stand history (Spies *et al.*, 1988), thus low levels of snags and the dominance of total CWD volume by large diameter jack pine logs in the 23 yrs stand can be explained by a low pre-fire stand density with a low proportion of jack pine, whether a long fire interval after the dead trees have fallen. We assume that large diameter snags and logs in the young stands were mostly of pre-fire origin while most small and medium-diameter snags resulted from the fire. The small diameter debris in the 48 yrs stand resulted from the first thinning wave that starts 25 yrs after stand regeneration according to Kenkel *et al.* (1997).

Premature and mature SRF stands (58-100 yrs)

Jack pine density was low in premature and mature stands compared to young stands, a trend consistent with that reported by Gauthier *et al.* (1993). This jack pine density decrease resulted from the process of stand self-thinning (Kenkel *et al.*, 1997), which lead to basal area increase observed in the mature stands (85, 95 and 100 yrs). Stem exclusion resulted in a peak of CWD volume in stands of 58 and 100 yrs. Understory biomass reached its maximum during this period and bryophytes expanded rapidly to become dominant. Possibly bryophytes started suppressing ericaceous growth. The understory vegetation heterogeneity in the young stands did not differ from the subsequent stages, which was contrary to Nguyen-

Xuan *et al.* (2000), who measured high species diversity in the recently burned black spruce stands (21 yrs since fire) and attributed high diversity to the abundance of propagules. It was possible that the young stands in our study, characterized by higher species diversity compared to the following stages. Although more detailed study of functional group diversity would allow to better understand understory development.

Old SRF stands (>118 yrs)

Canopy openness was lowest in the old stands due to the replacement of jack pine by black spruce and abundance of shade-tolerant deciduous species: *Alnus glutinous* L., *Betula papirifera* Marsh. and *Mespilus arborea* F. Michx. (*results not shown*). Similar gap-associated spruce regeneration has been observed in Sphagnum-Myrtillus stands of Eurasian south taiga forests (Drobyshev, 1999). Pines were sparsely distributed in old stands, and were represented by large and medium-diameter trees. No jack pine regeneration was found in the oldest stands (*data not shown*); small diameter jack pine density was inconsiderable either. This can be explained by the decrease of aerial seed banks reported by Pinard (1999) for old jack pines, unsuitable seedbed for this species germination (Greene *et al.*, 1999) and light deficit that limited seedling establishment (Gauthier *et al.*, 1996). It has been reported that senescence occurs in jack pine stands in the prolonged absence of fire (> 100 yrs) (Desponts and Payette, 1992), because jack pine attains its maximal life span at ca. 140 yrs (Van Wagner, 1978). In the absence of jack pine regeneration, the shift from pine to spruce occurred at approximately 150 yrs after SRF, as reported earlier (Gauthier *et al.*, 1993; Lecomte and Bergeron, 2005, 2006).

As expected based on previous studies (Sturtevant *et al.*, 1997; Brais *et al.*, 2005), CWD volume was highest in the old stands. Snag abundance was about six times superior to log abundance. Dead wood was represented by large-diameter debris resulting from jack pine senescence. Moreover as there was no recently-dead small-diameter regeneration, the amount of small-diameter CWD was insignificant. Log structural diversity was the highest along the

chronosequence. Conversely to it, snag structural diversity was lower compared to the younger stands.

Understory biomass was lower in the old forest compared to the premature and mature stands. In spite of bryophyte shade tolerance (Oechel and Van Cleve, 1986), deciduous tree litter accumulation can be a limiting factor for moss growth in old stands (Ipatov and Tarchova, 1980; Oechel and Van Cleve, 1986; Schimmel and Granström, 1997).

2.5.2 Non-stand replacing fire influence on jack pine stand structural development

Age evenness of the oldest cohort indicated that NSRF stands resulted from stand replacing fire of high intensity. The variation in the proportion of scarred trees and snags within NSRF stands confirmed the occurrence of moderate fire intensity gradient. However the evaluation of spatial pattern of the intensity gradient was not the objective of this study. Eventually the absence of a clear pattern of scarred tree distribution might result from their variation driven by the fire intensity gradient within NSRF stands.

Although it has been proposed that NSRF can initiate a second jack pine cohort (Desponts and Payette, 1992), the amount of small-diameter that may represent the second cohort was insignificant in NSRF stands. This may be due to the lack of adequate seedbeds, such as mineral soil or a thin organic layer that are less than a few centimeters thick (Greene *et al.*, 1999) because of superficial forest floor burning and insufficient insulation for seedling establishment. Analyses of fire scars on live trees and snags suggest that the NSRF that occurred in stands of 23 to 31 yrs caused high jack pine mortality. Low heat resistance of the cambium in the thin-barked young trees may explain this (Guyette and Stambaugh, 2004; Dickinson and Johnson, 2001). Jack pine mortality was lower when NSRF occurred in older stands, because of pine bark thickening. Thus, NSRF provided a stand thinning effect, which decreased inter-tree competition resulting in residual jack pine growth release. Also, one of

the major effects of NSRF was a delay of black spruce establishment in the canopy. NSRF injures already established black spruce individuals, and fast growing bryophytes may suppress black spruce post-NSRF growth. Similar NSRF effect on small diameter spruces has been reported for a multi-layered old-growth forest dominated by Scots pine (*Pinus sylvestris* L.) with the understory consisted of Scots pine and Norway spruce (*Picea abies* L. Karst.) in northern Sweden (Linder et al. 1998). Thereby, NSRF leads to increased jack pine density and life span compared to old SRF stands. This is consistent with NSRF effects reported by Weisberg (2004) for *Pseudotsuga menziesii* stands of western Oregon Cascade Range. NSRF developed a stand structure with highly variable tree diameters and abundance of large-diameter trees, an effect also reported by Rothstein et al. (2004) and Weisberg (2004). This confirmed our hypothesis that live tree structural diversity increased after NSRF.

NSRF decreased CWD volume and modified its diameter-class composition compared to SRF stands of comparable age, which confirmed our expectation of a NSRF rejuvenating effect on the stand structure. Fire scar analysis indicated that NSRF contributed to small-diameter tree mortality in the short term and possible large-diameter tree mortality in the long term. Nevertheless, NSRF diminished overall CWD accumulation because of a weakening of the self-thinning process. The decrease of stand development magnitudes was possibly the driving factor that resulted in similar CWD diversity in NSRF stands and inferior diversity compare to SRF stands.

NSRF initiated long-term, understory composition changes by injuring aerial parts of ericaceous shrubs and severely burning the lichens. However the understory regeneration could be explained by SRF. Thus, the proportion of ericaceous species decreased after NSRF, to the profit of bryophytes. Foster (1985) has reported a similar rapid dominance of bryophytes following low severity fires in Labrador. Fast regeneration of bryophytes can be explained by presence of residual canopy after NSRF consistently with reported by Schimmel and Granström (1997). Furtherdown, increase in canopy openness and higher volume of throughfall precipitation instead of stem flow, which becomes more available for the understory vegetation, also may lead to bryophyte dominance (Økland *et al.*, 2003). Also could It is also possible that a new addition of charcoal left by the NSRF resulted in an

indirect inhibition of ericaceous species due to the weakening of their competitive ability (Zackrisson *et al.*, 1996). Bryophyte dominance in NSRF stands homogenised understory structural diversity earlier than in SRF stands.

2.6 Conclusion

Structural succession in jack pine stands initiated by high intensity fires (SRF) can be outlined in three main stages: young stands (< 48 yrs), premature and mature stands (58-100 yrs) and old stands (>118 yrs). Non-stand-replacing fire (NSRF) in jack pine stands did not set back the clock of secondary succession to zero-moment, therefore resulting in a stand structure differing from that in SRF stands of comparable age. Among the most considerable effects of NSRF were: 1) delayed black spruce establishment in the canopy; 2) decreased dead wood volume; 3) increased bryophytes mass; 4) increased live tree structural diversity; and 5) decreased CWD structural diversity. Time since stand-replacing SRF was the time descriptor that apparently drove structural succession in NSRF stands by influencing the amount of structural legacies present. Our results suggest that forest management practices that imply stand thinning may result in undesirable bryophyte biomass increase. Conversely, NSRF influence on CWD and live tree structural diversity highlight the importance of disturbance magnitude on the functioning of the boreal ecosystem. It would thereby lend support to the development of variable retention logging systems. The lack of the information of pre-fire history hence black spruce development in the stands could be considered as major drawback of this study.

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CHAPITRE III

INFLUENCE OF STAND-REPLACING AND NON-STAND-REPLACING FIRE ON SOIL NUTRIENT ACCUMULATION AND CARBON SEQUESTRATION ALONG POST FIRE SUCCESSIONAL GRADIENT IN BOREAL JACK PINE STANDS[1]

Ce chapitre est la suite du chapitre II. Les sites étudiés sont les mêmes que dans le chapitre précédent. Alors que le chapitre II est dédié à l'impact du comportement du feu sur les structures résiduelles, le présent chapitre analyse l'impact des feux létaux et non létaux sur les processus du sol et sur la séquestration en carbone. Plus particulièrement, l'étude s'intéresse au rôle joué par les composantes ligneuses du sol forestier (bois enfoui) dans l'accumulation des éléments nutritifs. Nous nous attendons ici à ce que les feux non létaux entraînent un rajeunissement des peuplements de pins gris par rapport à des peuplements d'âge comparable issus de feux létaux.

3.0 Abstract/Résumé

Stand-replacing fires (SRF) drive structural succession in North American jack pine stands, although the presence of non-stand-replacing fires (NSRF) has been reported. NSRF modifies successional process in jack pine stands by changing live, dead tree and understory vegetation composition and forest floor and buried wood accumulation. The objectives of the study were: to document C sequestration in soil, coarse woody debris (CWD) and understory vegetation of jack pine stands as well as soil nutrient availability in relation to fire type and 2) to assess jack pine stand structure influence on organic matter and nutrient changes after two fire types, with buried wood being of special interest.

[1]Smirnova, E., Brais, S., Bergeron. Y. Influence of stand-replacing and non-stand-replacing fire on soil nutrient accumulation and carbon sequestration along post fire successional gradient in boreal jack pine stands[1] Submitted to the "Canadian Journal of Forest Research"

Stands affected by both SRF and NSRF were selected. Tree characteristics, understory vegetation, CWD and buried wood dry weight were measured; total nitrogen, phosphorus and exchangeable nutrients were determined in the forest floor, mineral soil and buried wood.

Mineral soil and live trees are the main carbon sinks in such stands. The concentrations of exchangeable nutrients decreased with time in the SRF stands. Non-stand-replacing fires in jack pine stands substantially decreased forest floor and buried wood C pool. Meanwhile, due to bryophyte biomass NSRF doubled the understory C pool. In these stands, N, P and CEC significantly differed from SRF stands.

Key words: carbon sequestration, exchangeable nutrients, fire intensity, coarse woody debris, lignic forest floor.

Les feux létaux (FL) dirigent les successions structurales des peuplements de pins gris nord-américains, quoique la présence de feux non-létaux (FNL) a été rapportée. Un FLN modifie les processus successionnels dans les peuplements de pins gris en changeant la composition des arbres vivants et morts, la végétation du sous-bois et l'accumulation de couverture morte et de bois enfoui. Les objectifs de l'étude étaient : 1) documenter la séquestration de carbone dans le sol, les débris ligneux grossiers (DLG) et la végétation du sous-bois des peuplements de pins gris et la disponibilité des nutriments dans le sol en lien avec le type d'un feu; et 2) évaluer l'influence de la structure des peuplements de pin gris sur la matière organique et le changement de nutriments après deux types de feu. Des peuplements affectés par un FL et par un FNL ont été sélectionnés. Les caractéristiques des arbres, la végétation du sous-bois, les DLG et le bois sec enfoui ont été mesurés. L'azote total, le phosphore et les nutriments échangeables ont été déterminés dans la litière forestière, le sol minéral et le bois enfoui.

Le sol minéral et des arbres vivants sont les principaux réservoirs de carbones dans les peuplements affectés par un FL. Les concentrations de nutriments échangeables n'ont pas montré de rapports significatifs avec le temps depuis un FL. Dans les peuplements de pins gris, le FNL diminue significativement le réservoir de carbone qu'est le bois enfoui et la litière forestière. En même tempes, FNL double la biomasse des bryophytes et, par conséquent, augmente considérablement la réserve de carbone dans la végétation du sous-bois. Dans les peuplements affectés par un FNL, l'azote, le phosphore et le CEC diffèrent significativement des peuplements affectés par un FL.

Mots clés : séquestration de carbone, nutriments échangeables, intensité de feu, débris ligneux grossiers, litière ligneuse.

3.1 Introduction

Fire in the boreal forest is the major natural disturbance, which initiates secondary succession, affects stand structure and changes nutrient cycling (MacLean *et al.*, 1983; Johnson *et al.*, 2000; Bergeron *et al.*, 2001; Sherriff and Veblen, 2006). Direct effects of fire on soil include loss of C, which can range from 5 % to 25 % (Harmon, 2001; Rothstein *et al.*, 2004) and nutrients through volatilization and convection (MacLean *et al.*, 1983) with decreases in soil nutrient pools (Brais *et al.*, 2000; DeLuca *et al.*, 2002). Indirect effects occur through modifications of soil temperature and moisture regime (DeBano, 2000); increases in organic matter decomposition rate (Rothstein *et al.*, 2004), nutrient availability (Viro, 1974), and leaching (MacLean *et al.*, 1983) as well as changes in soil biota succession (Pietikainen and Fritze, 1995; Sorokin *et al.*, 2000). It has been suggested that fire plays a rejuvenating role through the immediate release of nutrient but also through an increase in C-sequestration following the replacement of old-slow growing stand by young intensively growing stands (Peet, 1992; Rothstein *et al.*, 2004). It has also been reported that ash and charcoal deposited after fire optimize organic matter decomposition process (Zackrisson *et al.*, 1996; Saarsalmi *et al.*, 2001; DeLuca and Sala, 2006). However, immediate effects of fire on nutrient concentrations are of very short duration for boreal coarse textured soils (Brais *et al.*, 2000; DeLuca *et al.*, 2002; Smith *et al.*, 2004), while the magnitude of changes in soil nutrient and C pools were dependant on the severity of forest floor combustion (Brais *et al.*, 2000). Long term effects of fire on nutrient dynamics and sequestration through fire-induced changes in stand structures have yet to be investigated.

North American jack pine (*Pinus banksiana* Lamb.) stands are generally characterized by an even-aged structure resulting from high intensity fires (SRF stands) (Bergeron and Brisson, 1990; Gauthier *et al.*, 1993). However, the occurrence of non-stand-replacing fires (NSRF), which leave behind surviving trees, has also been reported (Desponts and Payette, 1992; Gauthier *et al.*, 1993). Investigating changes in stand structure induced by NSRF, Smirnova *et al.* (2008) found that NSRF decreased average stand density, coarse woody debris (CWD) also it delayed black spruce dominance and dramatically increased bryophyte

biomass. It has been suggested that fire type (Lecomte et al., 2006, 2007; Simard et al., 2007; Burton et al. 2007; Smirnova et al., 2008) greatly affected stand's live and dead biomass accumulation hence carbon sequestration and nutrient cycling. Also in these papers has been stressed that for better understanding the successional processes the consideration of all time descriptors: time since stand originating fire, time since non-stand replacing fire and the age, when the last fire had occurred, was important.

Stand structures such as live and dead trees, understory vegetation, coarse woody debris (CWD) and soil exert a large influence on ecosystem organic matter turnover and nutrient cycling. Characteristics feature of the boreal forest is substantial biomass accumulation in the understory layer and in the detritus: coarse woody debris, aignic and lignic forest floor (Oechel and Van Cleve, 1986; Harmon et al. 1986; Kayahara *et al.*, 1996; Sturtevant et al., 1997). Because as stands age, they reach a steady state characterized by slow growth of autotrophic organisms and increased C-retention due to detritus accumulation (Berg, 1986; Harmon, 2001; Chapin *et al.*, 2002). Understory species such as bryophytes can store large amounts of organic matter and nutrients and affect soil properties, increasing soil moisture, and decreasing soil temperature and affecting decomposition rate (MacLean and Wein, 1977; Oechel and Van Cleve, 1986; Boudreault *et al.*, 2002; Warlde et al., 2003; Fenton *et al.*, 2005; 2006).

CWD also act as reservoir of organic matter and nutrients. However, it has been suggested that despite the nutrients contained in CWD, its role as a nutrient source might be of minor importance compared to the forest floor (Laiho and Prescott, 2004) and mineral soil (Crawford *et al.*, 1997) as nutrients retained in CWD are characterized by slow turnover (Jurgensen *et al.*, 1997; Holub *et al.*, 2001; Laiho and Prescott, 2004). Nonetheless, these nutrients become available to plants through leaching to underlying soil horizons or through mycorrhyzal activity as roots are abundant in well decomposed dead wood (Means *et al.*, 1992; Jurgensen *et al.*, 1987; Crawford *et al.*, 1997; Tedersoo *et al.*, 2003; Brais et al., 2006). As well, CWD, including lignic forest floor within the forest floor, contribute to the accumulation of stable forms of humus in the soil that provide sites with nutrient retention

(Foster, 1974; Fisher, 1995; Prescott *et al.*, 2000). In stands with a low rate of organic matter decomposition, buried wood may account for up to 90 % of the Alignic forest floor mass (Brais et al. 2005). Whereas lignic forest floor influence on mineral horizons possibly depends on site moisture conditions (Kayahara *et al.*, 1996).

In this study we investigated and compared the effects of SRF and NSRF on carbon sequestration in live trees, CWD, lignic forest floor understory and soil.

The objectives of the study were: 1) to document C sequestration in live aboveground woody biomass, understory vegetation, necromass, and mineral soil; as well as soil nutrient availability along a chronosequence of jack pine stands following SRF, 2) to compare C-sequestration and soil nutrient status between stands affected by SRF and NSRF and assess the relationships between stand structure and these observed differences and 3) to assess the difference between forest floor and buried wood chemical properties, and to document buried wood influence on mineral soil properties. We expected that NSRF-induced changes in stand structures will reduce detritus C pool compare to SRF. We also anticipated that nutrient concentrations will not be altered considerably by NSRF compared to SRF stands. Lignic forest floor may cause small scale nutrient concentration enrichment.

3.2 Materials and methods

3.2.1 Study area

The study area is located in northwestern Quebec in the southeastern Canadian boreal forest. Climate is continental, with mean annual temperatures of 0.7 °C and mean precipitation of 937 mm (Environment Canada, 2004). The area is part of Precambrian Shield; Quaternary surface deposits cover most of the territory (Fig. 2.1). Soils from the study have evolved from coarse-textured glaciolacustrine deposits and are classified as humo-ferric podzols (perudic cryorthods) (Soil Classification Working Group, 1998).

3.2.2 Stand selection

Potential stands where first localized using the Quebec Natural Resources Ministry's forest inventory database which provides information such as stand composition, surface deposit, moisture regime and slope. All selected stands were dominated by jack pine with variable portion of black spruce (*Picea mariana* (Miller) Britton), paper birch (*Betula papyrifera* Marsh.) and sparse presence of balsam fir (*Abies balsamea* L.) and quaking aspen (*Populus tremuloides* Michx). Stands grew on coarse-textured soils with a fresh soil moisture regime and a slope ranging from 4 to 8 %. A nine jack pine stand chronosequence (approximately 10 years intervals) originating from stand replacing fire were selected based on an even-aged stand structure (Table 3.1).

Within or close to stands affected by SRF we selected eight stands that have survived non-stand replacing fire (NSRF) stands. Characteristic fire scar at the bottom of tree provided evidence of this fire type (Gutsell and Johnson, 1996). Stands that have survived NSRF can be dated according to the time since SRF (stand initiation), time since NSRF or stand age when NSRF occurred (Table 3.1).

Table 3.1 Characteristics of sampled jack pine stands on coarse-textured glaciolacustrine deposits.

Site code	Time since SRF	Time since NSRF	Stand age when NSRF occurred	Stand type	Mineral soil sand content (%)	Mineral soil silt content (%)	Mineral soil clay content (%)
H1	23	0	0	SRF1	81.2	11.2	7.6
H2	33	0	0	SRF1	91.4	2.2	6.3
H3	48	0	0	SRF1	79.2	22.9	2.2
H4	58	0	0	SRF1	94.8	2.4	2.8
H5	69	0	0	SRF2	88.0	9.9	1.9
H6	76	0	0	SRF2	93.8	4.3	1.8
H7	85	0	0	SRF2	99.4	2.8	2.2
H8	100	0	0	SRF2	79.8	14.9	5.2
H9	118	0	0	SRF3*	71.0	23.1	5.7
M1	77	53	23	NSRF1	84.8	8.2	7.0
M2	83	52	31	NSRF1	97.2	0.6	3.4
M3	87	33	54	NSRF1	87.5	3.2	9.2
M4	94	52	42	NSRF1	85.5	10.4	4.0
M5	95	30	65	NSRF1	96.2	3.1	0.6
M6	143	86	57	NSRF2*	97.2	0.4	3.2
M7	154	87	67	NSRF2*	92.6	1.2	6.2
M8	154	86	68	NSRF2*	87.5	3.8	9.4

* data were not used in the comparison analysis

3.2.3 Field methods

Within each selected stand, five 200 m^2 circular plots (7.98 m radius), distant from each other by 50 m, were established. The circles formed a box with plots at each corner with one circle in the middle. All snags were measured (diameter at breast height (DBH) and height). The presence of scars was noted. Snags state of decomposition was estimated according to Imbeau and Desrochers's (2002) classification which includes five decay classes: (4) recently dead tree with sound wood and bark, no green foliage; (5) sound wood, no foliage; (6) sound wood, barkless, broken top with height at least 50 % of what is observed on live trees of same DBH class; (7) decomposed wood, broken top with height no more than 50 % of what is observed on live trees of same DBH class; (8) stump, height less than 2 m.

Downed wood volume (logs) was assessed by diameter and decomposition class along six 50 m-transects systematically established around the five circle plots and connecting their centres (300 m in total). Log decomposition class was assessed according to the five-class system described by Thomas *et al.* (1979) and based on structural characteristics of boles: (1) bark and wood sound, twigs present; (2): no twigs, branches and bark mostly intact, (3): bark detached or absent, log partly covered by mosses; (4): log oval, bark absent, wood soft; (5): log has no structural integrity and is partly located within the forest floor. Decomposition class 5 logs were sampled when they surpassed the level of the forest floor by the equivalent of half their diameter.

Within each plot and at a distance of 4 m (north, south and east) from the centre, three 0.5 m^2 quadrates were sampled. All alignic forest floor ($FF_{alignic}$) material down to the mineral soil was excavated by hand. Accordingly to Kayahara *et al.* (1996) material was classified as distinct wood residue (FF_{lignic}) or forest floor originating from fine litter or mosses ($FF_{alignic}$). Buried wood was weighed and sub-sampled for dry weight estimation and chemical analyses. Alignic forest floor material was sampled for the same purposes from a smaller 25 x 25 cm quadrate. Forest floor thickness was noted. A bulk sample of the 0-10 cm mineral soil was taken out of buried wood at the same location and an undisturbed 100 cm^3 soil core was collected for bulk density measurement. Buried wood and $FF_{alignic}$ samples were taken to the laboratory for moisture determination and chemical property measurements.

3.2.4 Laboratory methods

Dead wood analysis

CWD volume was deduced from field measurements. For snags volume, the truncated cone equation (Rondeux, 1993) was used:

$$V_{snags} = \pi Hs^2/12(D^2+d^2+Dd)^2 \quad (1)$$

where Hs-the snag height, D - snag diameter at the bottom, d-diameter at the top of the snag. Those dimensions were derived from the proportions:

$$D=Ht \times dbh/Ht-1.3, \text{ and } d=D\ (Ht-Hs)/Ht \quad (2)$$

where Ht is a tree height before breakdown, which was calculated basing on the Chapman-Richards equation:

$$Ht = (130+B_0(1-e^{-B_1 dbh}))^{B2}/100 \quad (3)$$

The equation operates with the set of the coefficients specifics for different ecological regions of jack pine growth (Brais *et al.*, 2005).

For log volume was applied Van Wagner's equation (1978):

$$V_{logs}= (5.234/\text{transsect length}) \times n \text{ of pieces} \times D^2 \quad (4)$$

CWD mass were assessed from CWD volume and wood density measurements.

A total of 181 snag samples and 206 log samples were analysed. Density analyses were done on three samples of snag and log by decomposition class per stand (n = 3*number of classes). Density of snag and log samples was determined by water displacement after immersion in paraffin (Brais *et al.*, 2005)

Total N in dead wood was determined calorimetrically after a H_2SO_4/H_2O_2 digestion (Richards, 1993); thereafter N concentration was assessed by Quickchem Method for total N (Zellweger Analytic Inc., Lachat Instruments Division, Milwaukee, WI). A 50 % C concentration was applied to dead wood (Alban and Pastor, 1993) and understory vegetation.

Soil analysis

Soil texture was determined by Bouyoucos hydromether method (McKeague, 1976). Forest floor and mineral soil samples were sieved (2 mm) and pooled within each sampled

plot (Table 3.1). Soil organic matter concentration was determined by loss on ignition (McKeague, 1976). Soil pH was measured in 0.01 M $CaCl_2$ (Hendershot et al., 1993). Soil samples were extracted with NH_4Cl-$BaCl_2$ (Amacher *et al.*, 1990). Exchangeable cations (Ca, Mg, K, Na) were determined by inductively coupled plasma atomic emission (ICP, Perkin-Elmer Plasma 40) and exchangeable acidity by titration (Metler DL-40). Effective cation-exchange capacity was calculated by summing base cations and exchangeable acidity. Available phosphorus concentration was determined by colorimetry following H_2SO_4/H_2O_2 digestion (Richards, 1993).

3.2.5 Statistical analysis

Relationships between dry weight of logs and snags, alignic and lignic forest floor and mineral soil properties, summed carbon pools and time since fire in SRF stands were assessed by means of linear regression analysis. Regressions were considered significant at 95 % confidence level ($p < 0.05$).

Differences in snag and log density and N concentrations by decomposition classes were assessed by means of the Tukey test, which is considered as the most powerful test for balanced design ANOVA (SAS, User guide, 1999).

In order to compare the influence of stand-replacing (SRF) and non-stand-replacing fires (NSRF) on stand structures and soil properties, stands were separated accordingly to time since the last fire (Table 3.1). The first group (SRF1) was composed of young stands: 23, 33, 48 and 58 yrs of SRF origin. The second group of SRF stands (SRF2) was composed of 69, 76, 85, 100 year old SRF stands. While the NSRF1 group included NSRF stands ranging from 77 to 95 yrs since SRF. However the NSRF1 group had also survived non-stand-replacing fires between 30 yrs and 53 yrs ago and, in that respect, they were similar to SRF1 type in terms of time since last fire. Therefore, similar properties in NSRF and SRF1 stands would indicate that NSRF have similar effects to those of SRF in the 20 to 60 year period

following fire while, similar properties between NSRF and SRF2 would indicate that NSRF have no effects on the soil properties. In the Table 3.1 the stands marked by an asterisk (*) were not included in the analyses because their time descriptors were not comparable. Thus time since SRF of the stand H9 did not correspond to the time since last fire in NSRF stands (M6, M7, M8).

Differences between types SRF1 and NSRF1 and between SRF2 and NSRF1 in (1) stand structures, (2) carbon pool and properties of (3) alignic forest floor, (4) lignic forest floor, (5) mineral soil underneath the alignic forest floor, and (6) mineral soil beneath lignic forest floor were tested by means of simple means comparisons (contrasts).

In order to assess buried wood influence on soil characteristics, means of buried wood and $FF_{alignic}$ properties as well as mineral soil properties of soil sampled underneath the buried wood and underneath the $FF_{alignic}$ were compared by means of T-test.

Data analyses were done using MEANS, REG, ANOVA, ttest, UNIVARIATE procedures of the SAS statistical package (SAS Institute Inc., 1999).

3.3 Results

In the studied stands all soils sand content ranged from 71 to 99 %, and clay content was less than 10%. Age of SRF stands ranged from 23 to 118 yrs. Stands that were affected by NSRF were first initiated by SRF between 77 yrs to 154 yrs ago; the subsequent NSRF occurred 31 to 87 yrs ago. All NSRF stands were subjected to NSRF before stand maturity, with the youngest stand 23 yrs after SRF and the oldest 67 yrs.

3.3.1 Changes in CWD characteristics along a stand-replacing fire-induced chronosequence

At the stand level, the snag density did not change significantly along a structural decomposition gradient. Among all decomposition class only logs of class 5 were characterized by a lower density. Densities were applied to their corresponding volume (Table 3.2).

The mean snag dry weight was 9.7 t ha^{-1} (std = 6.3) and the mean log dry weight was 2.4 t h^{-1} (std = 3.2). The minimum snag weight (< 0.1 t ha^{-1}) was measured in the youngest stand and the maximum weight (15.8 t ha^{-1}) in the 58 yr old stand. The minimum log dry weight (0.1 t ha^{-1}) was in the 85 year old stand and the highest in the 100 year old stand (10.07 t ha^{-1}). The data of snag and log volume in two youngest stands (23 and 33 yrs) were not included in the regression analyses. This was because the values were outstandingly low, which was contradictory to the results published for young stands (Brais et al., 2005). Therefore this raised the doubt about human intervention following fire in theses stands. No significant relationships between snag or log dry weights with time since SRF were found (*results not shown*).

Mean FF_{lignic} mass was 13.70 t ha^{-1} (std = 13.4) with maximal values in the oldest stand, where the buried wood mass was 50.8 t ha^{-1} (Fig. 3.1a). No significant relationship between alignic forest floor with time since SRF was found (Fig. 3.1b); its lowest values was in the stand of 60 yrs and the highest at age 118 yrs since SRF.

Table 3.2 Snags and logs density and N concentrations according to decomposition class. Analyses of variance and mean comparisons (Tukey test). Significant differences between classes are indicated by different letters.

Decomposition class	Density ($g\ cm^{-3}$), std	Tukey grouping
	snags	
4	0.45 (0.05)	A
5	0.45 (0.06)	A
6	0.43 (0.07)	A
7	0.44 (0.05)	A
8	0.46 (0.29)	A
Overall model	F=0.08, $p < .98$	
	logs	
1	0.40 (0.07)	A
2	0.41 (0.06)	A
3	0.36 (0.07)	A
4	0.37 (0.11)	A
5	0.24 (0.07)	B
Overall model	F=10.18, $p < .01$	

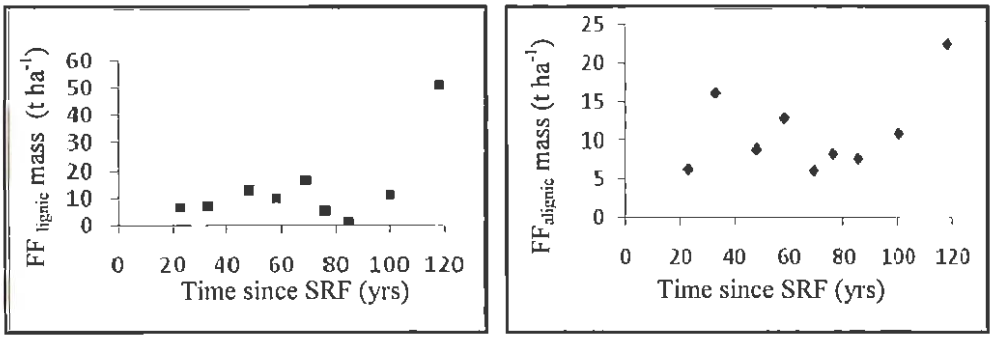


Fig. 3.1 a) Lignic forest floor (FF_{lignic}) (■) and b) alignic forest floor ($FF_{alignic}$) (♦) dry weight in relation to time since SRF

3.3.2 Changes of soil nutrient status along a stand-replacing fire-induced chronosequence

Forest floor pH averaged 2.8 (std = 0.2), and did not change significantly with time since fire. Significant relationships were found between $FF_{alignic}$ N and Mg concentrations and time since SRF (Fig. 3.2a,b) while, no significant trend in organic C, C/N, exchangeable Ca and K and available P concentrations in forest floor originating from fine litter was observed along the chronosequence (see table 3.3a for average values by stand groups).

Buried wood Kjeldahl N concentrations, available P concentrations and CEC showed significant trends with time since SRF as Kjeldahl N and available P decreased linearly while effective CEC increased (Fig. 3.2c-e).

Mineral soil CEC and exchangeable Ca showed significant quadratic trends in relation to time since fire (Figs. 3.2f). Exchangeable CEC values decreased until 60 to 89 yrs and increased thereafter. Exchangeable Ca was described by a significant second order polynomial trend with time since SRF. The Ca concentration from the 118 yrs stand was removed from the analyses because a Cook's distance test indicated it as an outlier. Exchangeable K significantly increased with time since SRF; K concentration in the 100 yrs stand was also an outlier (Fig. 3.2h).

Table 3.3a. Effects of fire intensity on soil and buried wood properties in jack pine stands. ANOVA with contrast performed between SRF and NSRF stands. T-test performed on the lignic forest floor vs alignic forest floor and mineral soil vs mineral soil beneath lignic forest floor in grouped SRF and SRF stands. Bold italics indicate significant differences between stand groups.

Variable	Average values and population standard deviations				SRF1vs.NSRF1		SRF 2 vs. NSRF1	
	SRF 1	SRF 2	NSRF1	STD	F	*p*	F	*p*
alignic forest floor ($FF_{alignic}$) properties								
Mass (t ha^{-1})	11.09	8.25	9.74	5.23	0.15	.71	2.13	.13
C (g C kg^{-1}soil)	492.00	447.72	474.15	51.32	0.35	.56	0.33	.57
N (g N kg^{-1} soil)	11.48	7.04	9.57	2.31	3.22	.06	3.96	***.05***
C/N	42.86	63.59	49.54	16.24	6.72	***.04***	6.98	***.03***
pH	2.88	2.89	2.87	0.21	0.69	.35	0.69	.35
P (g PO_4kg^{-1} soil)	67.95	70.98	60.65	10.19	0.22	.64	0.02	.88
CEC ($cmol_c$ kg^{-1}soil)	26.62	26.98	22.59	2.44	7.07	***.03***	9.71	***.01***
Ca ($cmol_c$ kg^{-1} soil)	8.39	6.64	6.55	1.38	2.13	.14	0.04	.84
K ($cmol_c$ kg^{-1}soil)	1.77	1.67	1.67	0.15	0.54	.46	0.98	.33
Mg ($cmol_c$ kg^{-1} soil)	1.80	1.66	1.53	0.01	0.54	.47	0.82	.37
Exchangeable acidity ($cmol_c$ kg^{-1} soil)	13.81	15.61	12.52	1.76	5.71	***.02***	2.86	.09
lignic forest floor (FF_{lignic}) properties								
Mass (t ha^{-1})	9.28	8.84	10.03	0.57	1.52	.26	4.26	***.05***
C (g C kg^{-1} FF_{lignic})	468.56	476.46 *	466.62 *	16.29	0.03	.67	0.73	.41
N (g Nkg^{-1} FF_{lignic}	5.54 *	4.52 *	4.53 *	0.58	4.33	***.05***	0.17	.69
C/N	87.82 *	105.42 *	92.27 *	15.25	3.18	.10	0.40	.54
pH	2.66 *	2.65 *	2.79 *	0.08	0.06	.75	0.03	.82
P (g PO_4 kg^{-1} FF_{lignic})	36.05 *	29.27	37.46	3.69	0.01	.92	0.31	.59
CEC($cmol_c$$kg^{-1}$ FF_{lignic})	18.76 *	20.01	17.65	1.50	0.01	.91	4.25	***.03***
Ca ($cmol_c$$kg^{-1}$ FF_{lignic})	4.80 *	4.12	4.56	0.14	1.98	.19	<0.01	.95
K ($cmol_c$$kg^{-1}$ FF_{lignic})	0.88 *	0.95	0.86	0.05	0.06	.81	1.76	.09
Mg ($cmol_c$ kg^{-1} FF_{lignic})	0.73 *	1.02	0.98	0.12	6.93	***.03***	1.82	.21
Exchangeable acidity ($cmol_c$ kg^{-1} FF_{lignic})	10.89	13.90	11.23	1.47	156	.24	1.79	.13

* *p* values of t–test of alignic forest floor vs lignic forest floor and mineral soil vs mineral soil beneath lignic forest floor within each stand types are different at the 0.05 level

Table 3.3a (cont)

Variable	Average values and population standard deviations				SRF 1 vs NSRF1		SRF 2 vs NSRF1	
	SRF 1	SRF 2	NSRF1	STD	F	*p*	F	*p*
			mineral soil properties					
pH	2.97	3.08	3.09	0.07	0.24	.64	0.65	.44
C (g C kg^{-1} soil)	37.10	39.32	30.41	7.86	1.09	.32	0.05	.82
CEC (cmolc kg^{-1} soil)	2.26	2.96	3.60	3.60	3.29	***.05***	0.15	.71
Ca (cmolc kg^{-1} soil)	0.25	0.21	0.39	0.09	4.45	.06	8.36	***.02***
K (cmolc kg^{-1} soil)	0.60	0.06	0.11	0.03	2.31	.16	0.10	.99
Mg (cmolc kg^{-1} soil)	0.01	0.04	0.09	0.04	9.97	***.01***	3.34	***.05***
Exchangeable acidity (cmolc kg^{-1} soil)	2.60	2.98	2.99	0.23	1.77	.19	<0.01	.97
			mineral soil properties beneath lignic forest floor					
pH	2.86	2.92	3.10	0.18	3.76	***.05***	2.89	.09
C (g C kg^{-1}soil)	29.52 *	29.15	27.81	9.31	0.07	.80	<0.01	.96
CEC ($cmol_c$ kg^{-1} soil)	3.13	3.31	3.41	1.04	0.52	.47	0.13	.72
Ca ($cmol_c$ kg^{-1} soil)	0.26*	0.38	0.32	0.02	0.67	.42	2.88	.09
K ($cmol_c$ kg^{-1} soil)	0.10 *	0.10 *	0.10 *	0.01	0.17	.68	0.34	.56
Mg ($cmol_c$ kg^{-1} soil)	0.04	0.06	0.04 *	<0.01	1.64	.12	0.29	.43
Exchangeable acidity ($cmol_c$ kg^{-1} soil)	2.85	3.16	2.91	1.08	0.07	.80	0.27	.61

* *p* values of t–test of alignic forest floor vs lignic forest floor and mineral soil vs mineral soil beneath lignic forest floor within each stand types are different at the 0.05 level

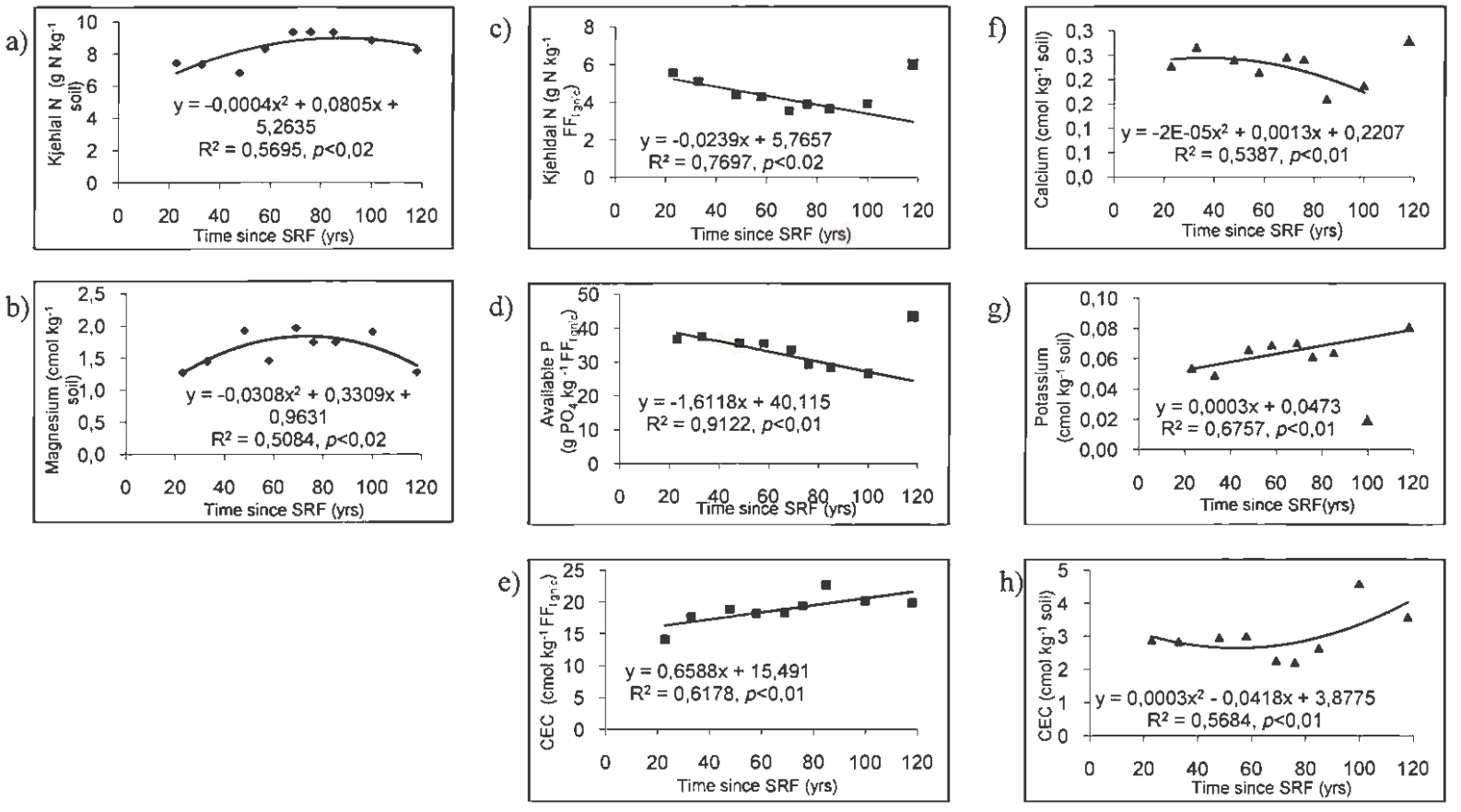
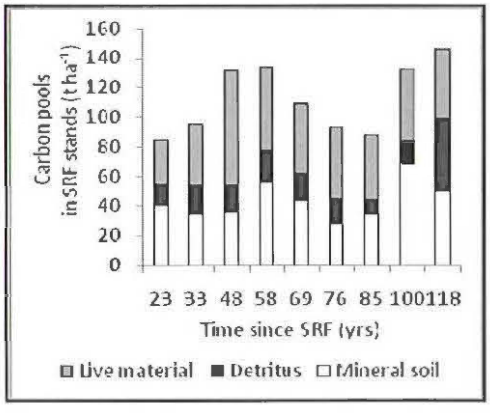


Fig. 3.2 Relationships between N concentration, Ca, K, Mg, P and CEC and time since last fire: in alignic forest floor (a, b) (♦), lignic forest floor (c to e) (■) and in the mineral soil (f to h) (▲). Only significant relationships are shown; the outliers are not included in the regressions.

3.3.3 Changes in C pools and time since stand replacing fire

Total carbon pool was at its lowest in the youngest stand (23 yrs) and attained a maximum of 186.0 t ha^{-1} in the oldest stand (Fig. 3.3a). Mineral soil and live biomass formed the two largest carbon pools. Live tree carbon pool was about ten times higher than understory pool (Table 3.3b). In the detritus pool, the buried wood portion was the most substantial.

a)



b)

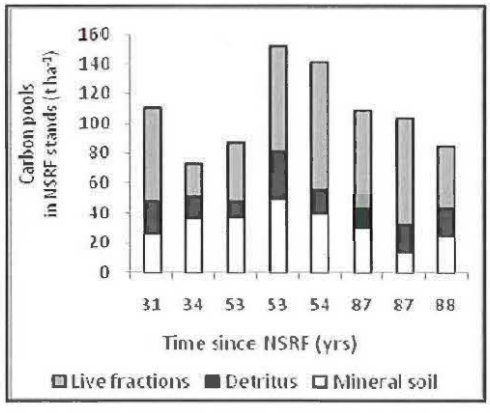


Fig. 3.3: a) Carbon pools in SRF stands; b) Carbon pools in NSRF stands.

3.3.4. Effects of non stand-replacing fire on lignic forest floor and mineral soil properties and carbon sequestration.

In the 23-58 year period following fire, NSRF had effects on alignic ($FF_{alignic}$) and lignic forest floor (FF_{lignic}) , and mineral soil that differed from those of SRF (SRF1, SRF2) (Table 3.3a). Thus in NSRF1 N concentration in the $FF_{alignic}$ was higher (at the $p = 0.1$ level) compared to SRF2; while C/N ratio in NSRF1 was higher than in SRF1 and lower than in SRF2.

In the $FF_{alignic}$ non-stand- replacing fire also resulted in lower effective CEC, acidity and exchangeable Mg concentrations compared to both SRF groups. In the lignic forest floor N concentrations in NSRF1 was lower compared to SRF1; effective CEC and exchangeable Mg in NSRF1 were lower compared to SRF2 stands.

Mineral soil effective CEC and exchangeable Mg concentration were higher in NSRF1 (at the p= 0.1 level) compared to SRF1; also Mg concentrations were higher in NSRF1 compared to SRF1. Exchangeable Ca concentrations were higher in NSRF1 compared to SRF.

A NSRF occurring in mature stands (NSRF1 vs SRF2) increased FF_{lignic} mass by 13 %, while decreasing its effective CEC by 12 %. It also resulted in an increased in $FF_{alignic}$ N while decreasing its C/N ratio, effective CEC and exchangeable acidity. A NSRF also increased mineral soil exchangeable cation (Ca, Mg) concentrations. However, exchangeable Ca concentrations were lower beneath the buried wood.

Similarly to what was observed in SRF stands, mineral soil and live material represented two major C pools in NSRF stands (Fig. 3.5b; Table 3.3b). In SRF stands C retained in live trees was lower compared to NSRF stands. Stands affected by NSRF had more C retained in the understory biomass than stands initiated by SRF (NSRF1 vs. SRF2, Table 3.3b), while C retained in snags and mineral soil was higher in the absence of NSRF.

Table 3.3b. Effects of fire intensity on stand structures and carbon pools in jack pine stands. ANOVA with contrast performed between SRF and NSRF stands. Bold italics indicate significant differences between stand groups.

Variable	Average values and population standard deviations				SRF1vs.NSRF1		SRF 2 vs. NSRF1	
	SRF 1	SRF 2	NSR1	STD	F	*P*	F	*p*
	carbon pools (t ha^{-1})							
Total	107.52	105.78	112.73	26.67	1.66	***.04***	1.78	***.04***
Live trees	49.11	42.98	52.53	18.23	2.81	***.04***	4.46	***.01***
Total understory	1.98	3.02	3.65	1.55	5.06	***.05***	0.92	.37
Bryophytes	1.02	1.46	2.30	1.55	1.06	.19	2.89	***.05***
Ericaceae	0.91	1.07	0.88	0.54	0.01	.92	0.21	.66
Snags	6.42[1]	2.91	3.80	2.79	3.01	***0.5***	0.46	.52
Logs	2.70[1]	2.05	2.82	1.69	0.99	.26	0.15	.71
Alignic forest floor ($FF_{alignic}$)	5.55	4.13	4.79	2.42	1.52	.26	1.24	.35
Lignic forest floor (FF_{lignic})	5.38	5.13	5.63	6.48	0.50	.50	0.74	.08
Mineral soil	41.85	48.53	37.56	12.98	0.50	.50	2.74	***.04***

[1] Stands of 48 and 58 yrs since SRF.

3.3.5 Effects of lignic forest floor on mineral soil properties

Nitrogen concentrations of the lignic forest floor were more than three times higher than that of logs of decomposition class 5 (5.1 g N kg^{-1} and 1.5 g N kg^{-1} respectively). Differences between lignic and alignic forest floor were more apparent in SRF1 stands than in the other two types. This is where its effects on mineral soil properties were also more pronounced. In SRF1 stands pH, CEC as well as concentrations of available P and exchangeable Ca, K and Mg were significantly lower in the lignic forest floor than in the alignic forest floor (Table 3.3b); contrary, the C/N ratio was significantly higher in FF_{lignic}. In SRF1 the range in C concentration in FF_{lignic} was similar to $FF_{alignic}$ (Table 3.3b). In SRF2 concentrations of C and C/N ratio was higher in the lignic forest floor FF_{lignic}, while pH and N concentrations were lower than that of $FF_{alignic}$. Ultimately, after the passage on non-stand-replacing fire C and N concentrations were higher in the $FF_{alignic}$; while lignic forest floor had higher C/N ratio and pH.

Mineral soil organic C and exchangeable Ca were lower beneath the lignic forest floor in SRF1 stands only. The lignic forest floor increased exchangeable K in mineral soil regardless of stand type and increased exchangeable Mg in NSRF stands only.

3.4 Discussion

3.4.1Exchangeable nutrients

Several studies have documented changes in soil nutrient availability along successional gradients in the boreal forest (Van Cleve *et al.,* 1991, Paré *et al.*, 1993, Brais *et al.,* 1995; Neff *et al.*, 2005). They have shown a decline in nutrient availability, especially of N, which is related to succession from deciduous to coniferous species. Jack pine stands are characterized by low plant diversity while little changes in composition take place during succession. The main successional trends in vegetation observed following SRF were an

increase in black spruce density, decrease in canopy opening and ericaceous biomass (Smirnova *et al.*, 2008). Coniferous litter of poor quality is characterized by high lignin to nitrogen ratios and slow organic matter decomposition (Berg and Meentemeyer, 2002). Ericaceous species are also known for their relatively poor organic matter quality. It might not be surprising that contrary to studies (Van Cleve *et al.*, 1991, Paré *et al.*, 1993, Brais *et al.*, 1995; Neff *et al.*, 2005) we found little changes in nutrient concentrations of alignic forest floor along 100-years (from 23 to 118 yrs since SRF) fire-induced succession.

Lignic forest floor and mineral soil showed stronger trends with time. Stand maturity (60 to 80 yrs) seemed to be the turning point where buried wood concentrations increased while that of the mineral soil decreased although the nutrients involved were not the same for the two horizons excluding nutrient transfer from one horizon to the other. The turning point also coincided with increases in buried wood, alignic forest floor and black spruce basal area and a decreased in ericaceous abundance.

Consistently with our hypothesis, NSRF effects on alignic forest floor nutrient availability did not differ substantially from SRF in the 20 to 60 year period following fire. This was in accordance with Miyanishi and Johnson (2002) who have suggested that fire intensity was not related to the smouldering combustion occurring in the soil. However, alignic forest floor and buried wood N concentrations in NSRF stands were lower compared to young SRF stands. DeLuca and Sala (2006) also reported that repetitive fires can decrease alignic forest floor N concentrations. In older stands that have survived a second fire (NSRF), mineral soil divalent cation concentrations were much higher than those observed in young SRF stands indicating a rejuvenating effect of NSRF.

Exchangeable Mg and, to a lesser extent, Ca were the mineral soil nutrients most affected by fire type. Charcoal deposition resulting from NSRF could explain higher concentrations of these cations in the mineral soil. Lehmann *at al.* (2003) have reported that due to its chemical and physical properties charcoal may decrease Ca and Mg leaching. While during the time

since NSRF (30-53 yrs) charcoal influence on the alignic forest floor might became undetectable.

3.4.2 Lignic forest floor (buried wood)

Buried wood properties and dynamics have so far received little attention (McFee and Stone, 1966; Harvey *et al.*, 1981; Means *et al.*, 1992; Kayahara *et al.*, 1996; Brais *et al.*, 2005). Fire may directly generate buried wood when snags fall immediately after fire. However, jack pine snags over 100 year old have been reported in fire history reconstruction study in the region (Dansereau et Bergeron 1993) and gradual fall of burned snags in the course of succession may increase the variability in logs and buried wood decay. Half-life of decaying jack pine logs was estimated to be 35 years (Brais et al., 2006) and it might take years before all above-ground dead wood is incorporated into the forest floor. Charring and wood seasoning may also delay above-ground dead wood decomposition (Harmon et al. 1986). However, buried wood was in a more advanced stage of decay than that of the overlaying logs as shown by its lower C/N ratio (assuming a carbon concentration of 50% for logs).

Buried wood characteristics are different from those of alignic forest floor and well decayed logs (decomposition class 5). Available nutrients and Kjeldhal N concentrations are lower in buried wood than in fine litter, while buried wood C concentration and C/N ratio are much higher, indicating a lower organic matter quality. However, the general decrease in N and P concentrations in buried wood with time since SRF indicate that buried wood is not acting as a sink for those nutrients. Brais *et al.* (2006) have shown that decomposing jack pine logs N and P concentration were increasing as decay proceeds but logs were a net source of N and P after a short initial period of net immobilisation. However, buried wood's capacity to act as a cation sink is increasing with time because of changes in colloidal properties. Nonetheless, buried wood is more acidic and provides less CEC than material originating from fine litter (Kayahara *et al.*, 1996; Spears *et al.*, 2003).

Buried wood formed a major portion of total forest floor in these boreal jack pine stands and was the most important C pool, after mineral soil, in SRF stands. Buried wood abundance significantly decreased after NSRF, because all NSRF stands were young (23 to 68 yrs), when NSRF has occurred (Table 3.1) therefore buried wood amount was low. Also, post-NSRF period in all NSRF stands was less than 86 yrs.

In accordance with Holub, (2001) buried wood significantly increased some nutrient concentrations in the underlying mineral soil. This effect might result from ectomicorrhizal activity: N and P fixation and element turnover caused by fine root colonization (Harvey *et al.*, 1981; Tedersoo *et al.*, 2003). Lower pH of buried wood could also favour nutrient leaching (Barber, 1995; Kayahara *et al.*, 1996). Because of its water retention properties (Brais *et al.*, 2005) and nutrient reservoir or weak resistance to root growth, buried wood can be a favourable substrate for fine root colonization.

3.4.3 Carbon sequestration

Live trees and dead wood C pool were within the range reported in the studies conducted in jack pine stands (Rothstein *et al.*, 2004, Lecomte *et al.*, 2006; Simard *et al.*, 2007). Similarly to Rothstein *et al.* (2004), live trees and the mineral soil carbon pools were the greatest in SRF stands. Despite having very similar as SRF effects on nutrient concentration in the stands of 20 to 60 yrs following fire, NSRF decreased log C pool and increased that of understory vegetation. Similar tendency has been reported by Hall et al. (2006) for moderate intensity fire in ponderosa pine stands. Low alignic forest floor accumulation in NSRF stands possibly resulted from bryophyte influence on decomposition processes, as bryophyte biomass was considerably superior compared to the SRF stands (Smirnova *et al.*, 2008). Accordingly to Schimmel and Granström (1997) remained canopies could favorite bryophyte establishment after non-stand replacing fires. Furtherdown, weak competition for the resources, in particular for the water, with other plants remained after fire may lead to the rapid bryophyte expansion, which has been already stated by: Titus and Wagner (1984),

Fenton and Bergeron (2006), Lecomte et al. (2006). Wardle *et al.* (2003) has reported that although bryophytes were characterized by low decomposition rate, bryophytes likely accelerate the decomposition of non-bryophyte litter. This could explain the observed in this study inferiour compared do SRF stands alignic forest floor accumulation after NSRF.

Dead wood and in particular buried wood and alignic forest floor formed two considerable C pools in the oldest stand. A similar trend was reported earlier by Harmon *et al.* (1986) and Sturtevant *et al.* (1997). Forest floor carbon accumulation occurred in coniferous stands because of high lignin content in coniferous litter, which decomposed slowly compared to the herbaceous or open-canopy litter (Berg, 1986; Prescott, 2005; Martens, 2000). Even though, CWD abundance was not maximal in the old stand, dead trees were characterized by large diameters. McFee and Stone (1966) stated that low decomposition rates of conifer debris appeared to be a main driving factor of buried wood accumulation. Moreover, lignin concentration increases with decay by brown rot fungi which remove cellulose and hemicelulose and leave lignin (Berg, 1986; Jurgensen *et al.*, 1987; Crawford *et al.*, 1997).

3.5 Conclusion

Post-fire succession, carbon sequestration and concurrent soil nutrient changes in pine ecosystems have been investigated earlier whereas, the influence of fire type: stand-replacing vs. non-stand-replacing fires and their impact on nutrient distribution an carbon sequestration has been largely omitted. Only few of soil properties have a significant relationship with time since stand replacing fire. The time descriptors of NSRF i.e. the time since stand establishing fire and time since NSRF differently affected soil properties. After both fire types: live trees and mineral soil formed the biggest carbon pools. While after a non-stand-replacing fire a portion of carbon sequestered in understory layer exceeded almost twice the one of the SRF stands, which was a particularity of NSRF stands. Considerable lignic forest floor accumulation is a distinctive characteristic of the boreal forest functioning. Although nutrient concentrations in the buried wood were lower than in the alignic forest floor originating from

the fine litter, lignic forest floor represents a considerable reservoir of nutrients in boreal soils.

Acknowledgments

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CONCLUSION GÉNÉRALE

Dans les écosystèmes forestiers boréaux, les fluctuations de l'ampleur et de l'intensité des feux expliquent en partie le type et l'abondance de structures résiduelles : abondance des arbres morts, des résidus grossiers, composition de sous-bois, horizon de litière, etc. Ces changements de structure résiduelle conduisent à une augmentation et à une diversification des habitats des organismes vivants, ce qui conduit à une augmentation de la diversité des espèces. La composition spécifique ainsi que la concurrence entre les individus sont les facteurs biotiques qui sont directement affectés par les feux. Ces facteurs biotiques évoluent avec le temps.

Les peuplements de pins gris sont en majorité caractérisés par une structure arborescente équienne résultant de feux létaux. Une infime proportion de peuplements ayant survécu à des feux non létaux a été reportée. La comparaison de l'impact de feux létaux et non létaux sur les structures de peuplement, la séquestration carbonée et les nutriments du sol et leur évolution au cours du temps n'ont encore jamais fait l'objet d'études chez le pin gris. L'aspect de l'étude lié aux fluctuations de la biomasse du bois enfoui après feu présente un intérêt certain pour ce projet.

Nos résultats montrent que, dans les peuplements de pins gris, les feux non létaux n'entraînent pas un retour de la succession secondaire à son stade initial. Cependant, les feux non létaux retardent le remplacement du pin gris par l'épinette noire alors que l'éclaircie des peuplements augmente l'abondance des arbres de gros diamètres et entraîne des changements dans l'abondance des débris ligneux, dans la proportion des différentes classes de décomposition et dans l'abondance de bois enfoui dans la couverture morte. Les feux non létaux augmentent la diversité structurale des peuplements et l'abondance des bryophytes. Par contre, leur effet rajeunissant sur les peuplements de pin gris, c'est-à-dire l'augmentation de la portion de carbone séquestrée dans la biomasse vivante et l'optimisation de la disponibilité

des éléments, n'a pas été confirmé dans cette étude. Les FNL diminuent les concentrations en cations basiques comparativement aux FL.

Par ailleurs, l'aspect de notre recherche qui a porté sur les interactions entre le degré de combustion de la canopée et celui de la mortalité des racines demeure une étude inédite. La relation entre la sévérité de la combustion de la couronne et l'ampleur des blessures des racines à la suite du feu mise en évidence pourrait contribuer au développement des modèles prédictifs sur la santé et la mortalité des arbres à la suite de feux de surface.

Les approches d'aménagement écosystémique récemment développées reposent, en partie, sur le principe que les pratiques forestières, soit la coupe sélective, la rétention d'arbres vivants ou morts, la préparation de sites, etc., pourraient maintenir des structures résiduelles similaires à celles observées après des perturbations naturelles (Franklin, 1993; Delong, 2002; Harvey et al. 2002). Toutefois, une meilleure et plus fine compréhension du gradient de l'amplitude des perturbations et des processus connexes de l'écosystème est encore essentielle pour améliorer les prescriptions sylvicoles. Les résultats de cette étude et particulièrement ceux obtenus au sujet du pin gris peuvent être appliqués du fait que les variations de la nature, de l'amplitude et de l'intensité des perturbations (feux, maladies causées par les insectes, chablis, etc.) affectent l'ensemble des éléments des diversités biologique, écosystémique, spécifique et génétique.

Effet indésirable des pratiques forestières : il pourrait se produire une baisse de la productivité du site et de la fertilité du sol comme conséquence de la coupe qui prélève une portion substantielle de la biomasse ligneuse (Lee et al., 2002; Hope et al., 2003; Bradley et al., 2006). La baisse de productivité peut être associée à une technique inappropriée de préparation de site ayant conduit à une perturbation insuffisante de la strate de sous-bois (Van Cleve et Viereck, 1981; McRae et al., 2001; Fenton et al., 2005). L'augmentation drastique de la biomasse des bryophytes à la suite des FNL pourrait être une preuve étayant ce phénomène. Cela pourrait être lié aux blessures superficielles causées par le feu dans le sous-bois. Aussi, la compréhension du processus de renouvellement du carbone et du cycle des

nutriments dans les écosystèmes boréaux en réponse aux perturbations naturelles pourrait contribuer à l'amélioration des pratiques forestières dans un contexte d'atténuation des émissions de carbone.

Conformément à ce que nous avions avancé antérieurement, la biomasse des bryophytes augmente substantiellement après un feu non létal. Cet effet pourrait se produire après une éclaircie précommerciale ou commerciale, des coupes sélectives et d'autres pratiques forestières qui supposent différents taux de rétention d'arbres, c'est-à-dire après une pratique forestière qui imite un feu non létal. Les incidences de ces phénomènes sur les propriétés du sol, notamment son régime thermique et hydrique, demandent à être étudiées.

Cette étude confirme que les éléments ligneux du sol forestier emmagasinent une quantité importante de nutriments. Il conviendrait donc d'étudier les éléments ligneux qui restent dans le sol forestier et d'évaluer leur contribution dans la productivité des peuplements, et ce, particulièrement pour les sols à texture grossière dont la rétention en eau et en nutriments repose sur leur contenu en matière organique.

La principale limite de cette étude porte sur l'absence de chronoséquences correspondantes entre feux non létaux et feux létaux. Il en est de même de l'analyse du gradient d'intensités de feux et de la mosaïque de blessures qui en découle ainsi que de la mosaïque de brûlures dans le sous-bois qui n'ont pas été abordées dans le cadre de cette étude. Toutefois, une telle étude aurait permis une meilleure compréhension des processus se déroulant au niveau du sol. Les analyses des éléments ligneux du sol forestier auraient permis une meilleure compréhension de la composition spécifique de ce dernier. De plus, une recherche plus axée sur l'analyse des éléments ligneux du sol pourrait permettre d'expliquer les processus de décomposition et de mieux comprendre le cycle des nutriments après le feu.

Le pin sylvestre du nord de la Suède et le pin gris de l'est du Québec sont deux espèces commerciales dominantes. L'amélioration des connaissances relatives aux effets des perturbations naturelles majeures de la forêt boréale sur l'évolution structurelle et les

processus écosystémiques chez le pin sylvestre et le pin gris présente non seulement un intérêt scientifique mais pourrait en plus être valorisée par l'industrie forestière.

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APPENDICE A

LES COORDONNÉES DES SITES D'ÉTUDES

Table A.1 The coordinates (UTM17) of the first circle on the study sites located in Quebec

Site	Year of SRF/ time since SRF (yrs)	Coord. X	Coord. Y	Precision
H1	1979 / 23	674341	5350770	9
H2	1969 / 33	675297	5439991	2
H3	1955 / 48	687186	5354946	18
H4	1945 / 58	708287	5364350	5
H5	1934 / 69	631259	5463243	6
H6	1927 / 76	708182	5367373	4
H7	1918 / 85	680115	5435231	6
H8	1903 / 100	679822	5435849	2
H9	1885 / 118	674423	5333307	3
H10	1854 / 149	785681	4919146	ni
H11	1848 / 155	785511	4953280	ni
M1	1927 / 77	706600	5372488	14
M2	1920 / 83	631391	5463365	6
M3	1916 / 87	632100	5462546	7
M4	1909 / 94	The stand has been cut off in 2003		
M5	1908 / 95	680590	5435556	1
M6	1863 / 143	673381	5442651	13
M7	1850 / 154	681684	5394090	30
M8	1850 / 154	632080	5462271	7

ni-no information